VOLUME LVIII NUMBER 1

THE
BOTANICAL GAZETTE

JULY 1914

THE MORPHOLOGY AND CYTOLOGY OF THE AECIDIUM CUP

F. D. FROMME

(WITH PLATES I AND II AND EIGHT FIGURES)

Recent cytological investigations of the Uredineae have materially aided in clearing up the obscure points connected with their complex life history and development. The nature of the sexual processes involved in the transition from the gametophytic to the sporophytic (haploid to diploid) stages has received much attention, and, although the results achieved are somewhat conflicting on minor points, the general nature of the phenomena described by the different authors is quite uniform. Although examples of both the caeoma and cup types of aecidia have been studied from this standpoint, the most clear and acceptable accounts have been given for the less complicated, superficial caeomas. No comprehensive cytological account of the stages in cup-formation or of the general morphology of the aecidium has been given. Certain authors also disagree as to whether the nuclear divisions are all mitotic or in part amitotic.

So far sexuality has been reported in 13 species of rusts; 11 of these cases may be regarded as well established for the present, but the remaining 2, *Uromyces Poae* and *Puccinia Poarum*, as reported by BLACKMAN (**6**), must be considered as doubtful or at best not entirely understood, since only a few inconclusive fertilization stages were seen. Of the remaining 11 cases, 9 are forms that have aecidia or primary uredosori in their life cycles, and 2 are forms that

lack aecidia. Of the first group, 2 species have aecidia of the cup type and 5 have aecidia of the caeoma type; while the remaining 2 have primary uredosori that have been shown to be functional aecidia. The 2 forms that lack aecidia are short-cycled microforms. Of these 11 species, 10 are autoecious and one (*Melampsora Rostrupi*) is heteroecious.

TABLE I

SUMMARY OF FERTILIZATION PHENOMENA

Species	Author	Date	Length of cycle	Type of aecidium	Method of fertilization
Phragmidium violaceum....	Blackman	1904	0, I, II, III	Caeoma	Nuclear migrations
Phragmidium speciosum....	Christman	1905	0, I, III	Caeoma	Equal cell fusions
Melampsora Rostrupi.....	Blackman and Fraser	1906	0, I, II, III	Caeoma	Equal cell fusions
Phragmidium Pot. canadensis	Christman	1907	0, II^1,II^2,III	Primary uredo	Equal cell fusions
Caeoma nitens..	Olive	1908	0, I (?)	Caeoma	Equal cell fusions
Triphragmium Ulmariae....	Olive	1908	0,II^1,II^2,III	Primary uredo	Equal cell fusions
Puccinia transformans.	Olive	1908	0, III		Equal cell fusions
Caeoma nitens..	Kurssanow	1910	0, I (?)	Caeoma	Equal cell fusions
Puccinia Falcariae....	Dittschlag	1910	0, I, III	Cup	Equal cell fusions
Endophyllum Sempervivi...	Hoffman	1912	0, I	Cup	Equal cell fusions
Melampsora Lini.....	Fromme	1912	0, I, II, III	Caeoma	Equal cell fusions
Puccinia Malvacearum	Werth and Ludwigs	1913	(0?), III		Equal cell fusions

In 10 of the cases reported the fertilization processes described are essentially of the type that involves a complete cell fusion between two equal gametes as originally described by CHRISTMAN for *Phragmidium speciosum*. In the remaining case, *Phragmidium violaceum*, as described by BLACKMAN, two cells are also involved in the fertilization, but these cells were held to be morphologically unequal and complete cell fusion was not observed. Nuclear migrations apparently similar to those described by BLACKMAN, but variously placed in the hyphae, have been reported by CHRISTMAN, KURSSANOW, OLIVE, and the writer, and were interpreted as pathological phenomena. The 10 cases of equal cell fusions are described by 7 different authors, and none of these has found true

fertilizations of the type described by BLACKMAN. OLIVE (22), however, reports and figures cases of fertilizations in *Caeoma nitens* (*Gymnoconia interstitialis*) and *Triphragmium Ulmariae* that suggest the nuclear migrations of BLACKMAN, but are in reality, as he says, simply early stages in cell fusion in which the connecting pore is as yet small. This pore enlarges subsequently and complete union of the cells is accomplished.

A summary as to the fertilization phenomena in the 11 species where fertilization has been described to date is given in table I.

Besides the question of sexuality, there are a number of unsettled points relating to the morphology of the aecidium cup. Some of these questions were raised by DEBARY and have as yet not been completely settled. For example, does the cup enlarge by the addition of new spore chains between those previously formed, or are the new chains added at the lateral borders? Is the peridium formed from the peripheral chains only, or are the central chains also involved? Do buffer cells similar to those found in the caeomas also occur in the aecidium cup?

DEBARY (4) stated that the hymenium of *Aecidium Berberidis* broadens before the cup completely matures, but was unable to determine how this was brought about. He states that the peridium arises from the marginal "basidia," and the entire outer chains composed of peridial cells arched over the center of the cup to form a covering over the central spore chains. RICHARDS (27) found that the growth of the hymenium was largely at the periphery and that only rarely were new chains added between those already formed. He states that the peridium is formed from the apical cells of the central spore chains and from all of the cells of the peripheral chains. The peridial cells are first formed at the center, and they are successively formed on all sides of this center until a complete protective layer is formed over the entire mass of spores. OLIVE (23) agrees substantially with RICHARDS as to the method of formation of the peridium.

The work of RICHARDS, BLACKMAN, CHRISTMAN, OLIVE, KURSSANOW, and others has been summarized by DITTSCHLAG (10), HOFFMAN (15), MAIRE (19), and the author (12), and therefore only the more recent papers will be reviewed.

DITTSCHLAG (10) was the first to describe sexual fusions in an aecidium of the cup type. He found cell fusions at the base of the young aecidium of *Puccinia Falcariae*, but was unable to trace completely the origin of the fusing cells. A single sterile cell was sometimes found above each gamete, but was not always present. Trinucleated basal cells were found that apparently arose from the fusion of three cells, and these basal cells gave rise to chains of trinucleated aecidiospores and intercalary cells. He further described branching basal cells for the first time. The primary basal cell formed a bud on the lateral wall, and two daughter nuclei from the preceding conjugate division passed into the bud. The bud enlarged further and then the nuclei proceeded to divide and give rise to a second chain of spores. His description of the origin of the peridium agrees with that of RICHARDS.

HOFFMAN (15) studied the development of the aecidium of *Endophyllum Sempervivi*, a species that completes its life cycle with the production of a single spore form, an aecidio-teleutospore, besides the spermatia. He distinguished two kinds of tissue in the young cup. The first tissue formed disintegrated to provide room for the development of the spores, and a second tissue, the "Paarungsgewebe," was then formed at the base of the primordium. The cells of this tissue were conspicuous for their size and the density of their cytoplasm, and were borne in filaments that had their long axes parallel to the surface of the leaf. Fertilization was accomplished by the dissolution of the adjoining cell walls between two gametes and perpendicular basal cells resulted. He also found triple cell fusions and trinucleated basal cells and spore chains. He thinks that one of the nuclei in a trinucleated spore eventually disintegrates, but obtained no convincing evidence of this. He also found branching basal cells like those described by DITTSCHLAG, and states in addition that the conjugate nuclear division that precedes the formation of the branch produces two pairs of nuclei of unequal size. The smaller pair enters the branch and the larger pair remains in the original half of the basal cell. His figures of this process are not at all convincing.

The author (12) has described the nuclear development of the

caeoma of *Melampsora Lini*. This form differed in structure from previously described caeomas in that two sterile cells were normally produced above each gamete. Equal cell fusions were found in abundance. A number of three and a few four-cell fusions were found, and these gave rise to chains of three and four-nucleated aecidiospores and intercalary cells. Multinucleated cells, whose origin and fate were not determined, were also found among the spore chains.

TABLE II

PLURINUCLEATED CELLS

Author	Date	Rust	No. of nuclei to a cell	Kind of cell
Sappin-Trouffy	1896	Ur. Betae	4	Uredospore
Blackman and Fraser	1906	P. Malvacearum	3	Teleutospore and basal cell
Blackman and Fraser	1906	Ur. Ficariae	3	Teleutospore
Blackman and Fraser	1906	P. Poarum	3 and 4	Aecidiospore initial cell
Blackman	1904	Ph. violaceum	3	Basal cell
Olive	1908	P. Cirsiil-anceolati	Up to 15	Cell at base of aecidium
Dittschlag	1910	P. Falcariae	3	Aecidiospores and basal cells
Hoffman	1911	Endo. Sempervivi	3	Aecidiospores and basal cells
Fromme	1912	Mel. Lini	3 and 4 3, 4, and 11	Aecidiospores Basal cells

WERTH and LUDWIGS (**28**) studied the teleutosorus of the microform *Puccinia Malvacearum*. They found cell fusions between the tips of club-shaped hyphae. The fusing cells were usually of unequal size and the nucleus of the smaller passed over into the larger. This binucleated cell cut off two cells, the lower of which became the stalk, and the upper, after a division, the two-celled teleutospore. They occasionally found binucleated cells in the vegetative tissue and were unable to explain their presence.

The occurrence of plurinucleated cells in the rusts is of some interest, since the uninucleated and binucleated condition seems to be very constant in the gametophytic and sporophytic mycelium, respectively. A number of instances of plurinucleated cells that have been figured by various authors are tabulated in table II.

Material and methods

The aecidia included in this study were collected during the spring and summer of 1912 in the vicinity of New York City and at Woods Hole, Massachusetts. Some 20 different species of aecidia were fixed and examined, and the most favorable were selected for a more detailed study.

The 6 species treated here are *Puccinia Claytoniata* Peck on *Claytonia virginica*, *P. Violae* (Schum.) DC. on *Viola papilionacea*, *P. Hydrocotyles* (Link) Cke. on *Hydrocotyle umbellata*, *P. Eatoniae* Arthur on *Ranunculus abortivus*, *P. angustata* Peck on *Lycopus virginicus*, and *Uromyces Caladii* Farlow on *Arisaema triphyllum*. I am indebted to Dr. J. C. ARTHUR for the identification of the aecidia.

Some of these species have been previously studied from the standpoint of sexuality. The aecidium of *Ur. Caladii* has been studied by RICHARDS (**27**) and by CHRISTMAN (**9**). RICHARDS has also studied an aecidium on *Ranunculus* that probably belongs to the same species as the one studied here. So far as I have ascertained, the remaining forms have not previously been studied cytologically.

Three of these rusts, *P. Violae*, *P. Hydrocotyles*, and *Ur. Caladii*, are eu-autoecious forms, that is, all four spore forms are included in the life cycle and all are borne upon the same host. Two of the other species, *P. Eatoniae* and *P. angustata*, are eu-heteroecious forms, the former with the uredosori and teleutosori on a grass, *Sphenopolis* (*Eatonia*), and the latter with these sori on a sedge, *Scirpus*. The remaining species, *P. Claytoniata*, is autoecious, but lacks the uredo stage. It belongs to the *opsis* group of SCHROETER'S classification and to the genus *Allodus* of ARTHUR'S (**1**).

In 3 of the species the aecidia are borne on a mycelium that is diffused throughout the tissues of the host. In the other 3 the mycelium is localized within a rather restricted area. These two types of aecidia can usually be distinguished at a glance. The aecidia from a diffused mycelium are distributed uniformly over the leaf or stem surface at approximately equal distances apart, and all on one part of the host are usually at the same stage of development. When the mycelium is localized, the aecidia are crowded

together in groups, often with an annular arrangement, and the older ones are found in the center of the group and the younger at the margins. This distinction is of some importance in collecting material for study, as it is usually necessary to make several collections of the forms from a diffused mycelium in order that all stages may be represented, while all stages may be present in a single fixation when the aecidia are from a localized mycelium.

All of the material was fixed in the field. Small segments of leaves or stems bearing aecidia were immersed immediately after removal in a small vial of fixing solution. Of a number of fixing solutions tested, weak and medium Flemming's were found to give the best results. The segments were allowed to remain in the fixative for 48 hours, after which they were washed, hardened, and imbedded in paraffin. The sections were stained for the most part with the safranin, gentian violet, and orange G combination, although iron-hematoxylin was used to some extent for comparative study.

The development of the cuplike aecidium

Puccinia Claytoniata proved to be an exceptionally favorable form for study. The cells and nuclei of the fungus are large, and the host tissue is soft and succulent and apparently permits rapid penetration of the fixing solution. The vegetative mycelium that precedes the formation of the spermogonia and aecidia is especially abundant and conspicuous. It is found in all of the leaf tissues, but is most abundant in the mesophyll near the lower epidermis. Most of the hyphae have their axis of growth in the long axis of the leaf. They are almost entirely intercellular except for the haustoria, which are short, knoblike, and usually penetrate only a short distance into the host cell. The hyphae are somewhat irregularly septate. The individual cells vary considerably in size. The average breadth is about 5 μ and the length three or four times the breadth. A single globular nucleus is located, usually, near the center of the cell; its diameter is but slightly less than the short diameter of the cell. The small nucleole stains a ruby red and is readily seen. The chromatin stains a deep blue and is distributed in small globular masses that are connected by delicate strands.

These often appear to be oriented on a point on the nuclear membrane, as OLIVE has found (**22**), but the presence of a central body was not ascertained with certainty. The hyphae branch monopodially at irregular intervals. The branch usually arises in the lateral wall near the apical end of the cell.

Binucleated cells were sometimes found in the vegetative mycelium, and continuous filaments of these were found in some cases. It is probable that the sporophytic mycelium had already established itself, and that both gametophytic and sporophytic mycelia were associated together in the same leaf tissue.

The aecidia are hypophyllous, and the first evidence of their formation is found in a conspicuous massing of hyphae between the lower epidermis and the cells of the first, second, and third layers of the mesophyll. The center of the young hyphal mass lies between the first and second cell layers. The hyphae are conspicuous on either side of this center for a distance of about two host cells. Thus the area to be occupied includes, in cross-section, 12 host cells, 4 cells broad and 3 cells deep. These host cells are gradually destroyed and replaced by the fungous hyphae.

The host cells in the center of the area are the first to disappear. The hyphae ramify between them, force them apart, and multiply in the intercellular spaces. They act as a wedge between the layers of host cells, and in forcing them apart produce a slight elevation of the epidermis. After these host cells have been completely cut off, they gradually diminish in size, and in most cases completely disappear eventually. The hyphae do not penetrate the host cells during their disintegration, and their disappearance seems to be due to the pressure brought to bear on them by the enlargement of the fungous mass. Their walls become much convoluted and infolded. The host cells are not always completely destroyed; sometimes they may be found imbedded in the tissue of an old aecidium.

In order that they may be described more clearly, the different surfaces of the hyphal mass will be designated as apical, basal, and lateral surfaces, the apical surface being that adjacent to the epidermis. This will apply to either an epiphyllous or hypophyllous aecidium. The individual filaments that make up the young

hyphal mass have their direction of growth toward the center of the mass, a point that usually lies between the first and second layers of host cells. In the very young stages the direction of growth is scarcely evident, since the hyphae wind around the intervening host cells; but as the host cells are crowded out and their site filled by branches of the surrounding hyphae or by others that force their way into the mass, it becomes more apparent. Not all of the hyphae are able to reach the center of the mass. Those on its lateral surfaces are crowded out by the earlier formed hyphae within and grow toward the epidermis, encircling the surface of the hyphal mass. There are 5 or 6 layers of these encircling hyphae.

The cells that make up the hyphal mass of the young cup are shorter and broader than those of the vegetative mycelium. Their cytoplasm is more dense and stains more deeply. This is particularly true of the cells of the interior, while those on the surface of the mass are less sharply differentiated from the purely vegetative cells. As the mass increases in size with the continued destruction of host cells, the fungous cells at the center begin to disintegrate. The first evidence of their disintegration is seen in the appearance of vacuoles in their cytoplasm. This is accompanied by the disorganization of the nucleus. They become detached from the hyphae on which they are borne and round up and enlarge to two or three times their original size if sufficient space is available. Some of these cells evidently undergo complete disintegration, while others become almost entirely empty except for a few cytoplasmic shreds and the remnants of the nucleus, and remain for some time in the center of the mass. They often become closely packed together as a result of enlargement, and have the appearance of a parenchyma. Because of this condition, this tissue of sterile cells is known as the pseudoparenchyma of the young cup (text fig. 1).

The first pseudoparenchyma cells formed are the apical cells of the hyphae that converge at the center of the hyphal mass. The disintegration of the cells of these hyphae proceeds from their apices toward their bases, and the area of pseudoparenchyma is increased by the addition of further cells on its margins. The apical surface of the mass is soon reached, and the sterilization of hyphae then

continues toward the lateral and basal surfaces. The hyphae that run from the basal surface of the mass to its center are on the average about 10 cells in length, while those that run from the lateral surfaces are somewhat shorter. Fig. 1 shows a section through the lateral surface of a young hyphal mass in which the sterilization of 3 or 4 of the apical cells of the hyphae has been accomplished. At the top of the figure the border of an epidermal cell, marking the apical surface of the mass, is indicated by a double line, and a cell of the mesophyll at the base of the figure indicates the basal surface. The cells beneath the pseudoparenchyma are shorter and broader than those on the lateral and basal surfaces of the mass, their

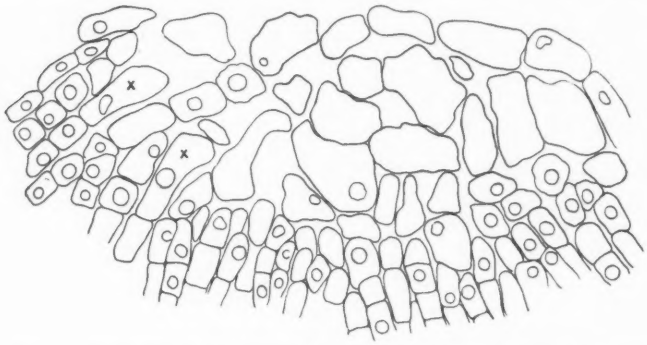

FIG. 1.—Formation of the pseudoparenchyma in the aecidium of *P. Claytoniata:* the attachment of the forming pseudoparenchyma cells (*x*) with the hyphae on which they are borne is evident.

nuclei are larger, with larger nucleoles, and their cytoplasm is considerably denser. Several layers of hyphae at the base of the figure that run tangentially to the curved basal surface of the mass are seen to give rise to the perpendicular hyphae that bear the differentiated, well nourished cells. The perpendicular hyphae shown in the figure average about 6 or 7 cells in length and have apparently cut off 3 or 4 sterile cells each. The sterilization process continues until only 4 or 5 cells at the bases of the perpendicular hyphae remain. The pseudoparenchyma is thus extended until it occupies about two-thirds or three-fourths of the vertical diameter of the mass. The remaining cells of the perpendicular hyphae now stand

out sharply from the pseudoparenchyma and the undifferentiated cells below them. Their cytoplasm is dense, their nuclei large, and the nucleoles especially large and prominent. They are apparently richly nourished at the expense of the cells of the underlying hyphae and vegetative mycelium. These richly nourished cells form a tissue, 2 or 3 cells in depth, that lines the inner basal surface of the young aecidium cup and extends for some distance upward on its lateral surfaces.

A comparison with the caeoma type of aecidium naturally suggests that these richly nourished cells are the gametes, and, as a matter of fact, practically all of the cells of this cup-shaped tissue may later fuse in pairs. Even though the fusion of all of them is not ultimately accomplished, the fusing pairs are distributed throughout the tissue and, before the fusions, those which are to fuse cannot be differentiated from the others.

These gametes of the aecidium cups of *P. Claytoniata* are quite comparable to the gametes of the caeomas. The aecidium of the caeomas is broad and shallow, and the gametes are produced in a single continuous layer beneath the leaf epidermis from which they are separated by a single layer of sterile cells only. They are the penultimate cells of the gametophoric hyphae. The aecidium of *P. Claytoniata* is spherical in shape and is deep-seated in the tissue of the host. The gametes form a tissue, 3 or 4 cell layers in depth, that lines the basal surface of the spherical mass. Above the gametes is found a tissue of sterile cells that has resulted from the disintegration of the upper two-thirds of the gametophoric hyphae. In the cup both the gametes and sterile cells form a tissue, while in the caeoma they form but a single layer. The sterile cells of the pseudoparenchyma and the "buffer" cells of the caeoma seem to be of similar origin and bear the same relation to the respective gametes above which they are borne. In both cases they are possibly potential gametes which have become sterile. If the sterile cells of the cup and the "buffer" cells of the caeoma are in reality homologous, BLACKMAN's conception, that the latter are morphologically trichogynes, would have to be extended to include a pluricellular type of trichogyne. It may be noted in passing that OLIVE (**22**) contends that the "buffer" cells are sometimes wanting

in *Caeoma nitens* and *Triphragmium Ulmariae*, and that according to my own observations (**12**) two "buffer" cells are normally produced above each gamete in the caeoma of *Melampsora Lini*. Further, I have found cases of two gametes borne one above the other in the same hypha in this form (**12**, pl. 9, fig. 18). *Melampsora Lini* thus seems to be an intermediate form between the more simple caeomas, with but one sterile cell and gamete to each hypha, and the aecidium cup with several sterile cells and gametes. It should be mentioned in this connection that the sterile cells of the cup can scarcely be considered to function as "buffer" cells in the sense that CHRISTMAN (**7**) used the term. If any function is to be ascribed to them, it is apparently that of space making. Their disintegration provides room for the development of the spores.

Up to this point in the development of the cup no multinucleated cells were seen, nor any other large cells that could in any way be considered central cells or organs from which the gametophoric hyphae might have arisen. Careful search was made for them in all stages in all of the forms included in this work, as well as in some additional forms. My observations do not agree, therefore, with those of MASSEE (**20**) as to the presence of central organs, nor with RICHARDS' (**27**) as to the presence of a "fertile hypha," nor do I find the multinucleated cells of OLIVE (**22**). I am confident that these multinucleated cells do not normally occur in any of the forms that I have studied. It is possible that they are peculiar to certain types of aecidia only.

The conditions found in the development of the aecidia of the other species investigated up to the time of the fertilization stage are very similar to those described for *P. Claytoniata*. Excepting minor differences, such as involve the form and size of the cup, its position in the leaf tissue, the relative extent of the pseudoparenchyma, and the number and position of the gametes, the general morphological development of all is of the same nature. The same excavation of the mesophyll of the host in areas of varying size and shape, and the same sterilization of radial hyphae to form the pseudoparenchyma are found in all.

The most noticeable difference found is in the position of the gametes. *P. Violae* is more like *P. Claytoniata* in this respect, and

in the general appearance of the sorus, than any of the others. The number and position of the gametes are practically the same in both. The sterile cells of *P. Violae* do not disintegrate so completely as do those of *P. Claytoniata*, and consequently form a more compact pseudoparenchyma. *P. Violae* is likewise a very favorable form for study, although the later stages do not fix so favorably as do the earlier ones.

In general appearance the early development of *Ur. Caladii* is much unlike that of the two foregoing species. The aecidium is much broader and shallower and is more superficially located in the leaf tissue. The young aecidium has the appearance of a deep-seated caeoma. The perpendicular gametophoric hyphae do not converge toward a central point in the young hyphal mass to such a noticeable degree, but run almost vertically toward the epidermis, a condition to be expected in a broad shallow sorus (text fig. 2). This condition of the gametophoric hyphae is more suitable to the study of the individual hyphae, and the sterilization of their apices and the position of the gametes are more easily seen.

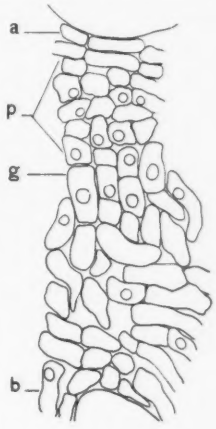

FIG. 2.—Section through the young aecidium of *Ur. Caladii: a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

The gametophoric hyphae consist of about 6 or 7 cells (text fig. 2). The upper 3 or 4 of these are sterilized and the remaining cells at the base are the gametes. As a rule, about two layers of gametes are formed, though in some cases there was apparently only one, and three were sometimes seen. The gametes are especially large at the time of fusion. The sterile cells do not disintegrate very completely prior to the fusions, and consequently scarcely any characteristic pseudoparenchyma appears. The aecidium is favorable for study, since both cells and nuclei are large. In comparing the sections of my material on *Arisaema* with RICHARDS' figures (**27**, figs. 1–4) of *Ur. Caladii* on *Peltandra*, it seems evident that the aecidium on

Peltandra is more spherical in form and less caeoma-like. My material of the aecidia on *Peltandra* was poorly fixed and only a few sections were cut. It is evident from these, however, that the general shape of the cup here is as RICHARDS has drawn it. A comparative study of the aecidia on these two hosts should be of interest in determining the relative influence of the host tissues on the morphology of the fungus.

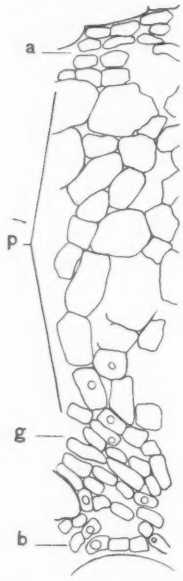

FIG. 3.—Section through the young aecidium of *P. Eatoniae: a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

The aecidia of *P. angustata*, *P. Hydrocotyles*, and *P. Eatoniae* are less favorable for study than any of the foregoing species. The cells of the young aecidia of these forms form a more compact hyphal mass, in which the direction of the individual hyphae is more difficult to trace. The pseudoparenchymatous tissue of all 3 forms is extensive and reaches to the lateral surfaces of the young aecidia, and to a deep point at their basal surfaces. My material of these forms was somewhat old, and the series of early stages is consequently less complete than in the case of the others. The directions of growth of the hyphae and their differentiation into the tissues of the cup are essentially similar to those described for *P. Claytoniata*. The gametes of these forms are not so sharply differentiated from the cells of the pseudoparenchyma and the underlying vegetative tissue, and often cannot be distinguished with certainty except when found fusing.

Since all my material of *P. angustata* was rather old, the gametes or fusion stages were not observed. The location of the two-legged basal cells seen (figs. 26, 27) seems to indicate that the gametes lie at the very bases of the perpendicular gametophoric hyphae. In *P. Eatoniae* the perpendicular hyphae are completely sterilized and the gametes are found in the upper two or three layers of the horizontal hyphae that line the basal surface of the hyphal mass. This

condition is illustrated in text fig. 3. The general direction of the hyphae on the lower border of the figure is tangential to the curved basal surface of the mass. These horizontal hyphae are present in all forms, and, as previously stated, give rise to the perpendicular hyphae. Fusions between cells of these horizontal hyphae are sometimes found in *Ur. Caladii*, but the gametes of this species are normally borne in the perpendicular hyphae. In *P. Eatoniae*, however, the gametes seem to be normally formed in these horizontal hyphae. *P. Hydrocotyles* is more like *P. Claytoniata* in the position of the gametes (text fig. 4). About 5 or 6 cells are found in the perpendicular hyphae below the pseudoparenchyma, and apparently any of the cells in this tissue may function as gametes.

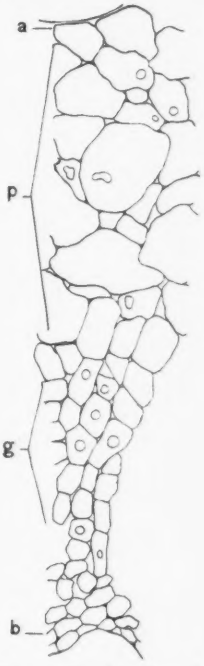

FIG. 4.—Section through the young aecidium of *P. Hydrocotyles*: *a*, apical surface; *b*, basal surface; *g*, gametic tissue; *p*, pseudoparenchyma.

Sexual fusions and spore-production

The fertilization in all these forms is accomplished by the fusion of two closely associated gametes that are normally equal in size and position. The first fusions are found in the central part of the gametic tissue, and the wave of fusions proceeds from this center toward the lateral borders of the aecidium. The fusions are quite abundant, and, though not so readily distinguishable as in the caeomas, many may be found in a favorable section (fig. 23). The process of fusion is identical with that found in the caeomas, and involves the dissolution of an area of the adjoining cell walls between two gametes. The gametes before the fusions are more or less differentiable by their size, the size of their nuclei, and the density of their cytoplasm. The nucleoles are especially large and conspicuous.

The dissolution of the walls may take place anywhere in the

region of contact between the gametes. They usually lie in parallel hyphae with their lateral walls in contact, and when they are in this position and are of equal height, the initial point of dissolution is usually near the middle of the cells or slightly above. A small pore is first formed. Figs. 4 and 5 are of early fusion stages between gametes of *P. Claytoniata*, and fig. 20 between those of *P. Violae*. As a rule, the dissolution of the walls continues on all sides of this pore until practically all of the adjoining walls have been dissolved away. Figs. 6, 16, 17, 21–24 show this condition in various forms. Fig. 23, of *P. Hydrocotyles*, is of especial note since three fusions are shown clearly within a small area. The figure shows further that the fusing cells have no definite position in the hypha or tissue in which they are borne. The two gametes on the right lie immediately beneath the pseudoparenchyma. Those in the center are considerably deeper in the tissue and are the third and fourth cells below the pseudoparenchyma of the respective hyphae in which they are found, while the pair on the left is placed midway between the others. A binucleated basal cell lies above the left gamete of this pair.

The fusions found in *P. Eatoniae* are different from those found in the other forms in that the gametes are located in horizontal hyphae at the base of the cup. A completed fusion between two such gametes is shown in fig. 24, and just above this lies the base of a two-legged basal cell. The upper part of the basal cell has been cut off in sectioning. The right gamete of the basal cell is the adjoining cell in the same hypha with the upper gamete of the fusion cell. Four layers of horizontal hyphae are found between the fusion cell and the host cell that marks the lower boundary of the sorus. According to HOFFMAN (**15**), the gametes of *Endophyllum Sempervivi* are also formed in horizontal hyphae near the base of the cup, and his figs. 1, 3, and 4 are very similar to corresponding stages in *P. Eatoniae*.

When the fusion of the gametes is completed, the fusion cell elongates in the direction of the epidermis and the nuclei move up into the central part of the cell (figs. 19, 22, 25–27). In *P. Eatoniae*, where the gametes lie in a horizontal position, the elongated part of the fusion cell often turns up at a sharp angle, as in fig. 25. The

cytoplasm of the fusion cells is more dense in the upper and central part and is often vacuolate in the base. For this reason it is often impossible to make out the two-legged character of an old fusion cell. Further, the fusion of the cells is often complete, and this also serves to make the detection of fusion cells more difficult in the cup aecidia than in the caeomas, where the fusion is usually between the tips of the gametes, and the bases remain distinct. After the elongation of the fusion cell, the nuclei divide conjugately in the upper central part. In the early stages of division the two spindles stand out sharply (fig. 10). They lie parallel to each other, with their poles in the long axis of the fusion cell. The process of mitosis was not studied in detail, but it seems evident, from the examination of a number of stages in both gametophytic and sporophytic cells, that the essential features are as described by OLIVE (**22**). The spindle figures in the early stages are very small. No central bodies could be differentiated at the poles and radiations were only rarely seen. Fig. 11 shows a late anaphase with the dumb-bell-shaped appearance that has been figured by many investigators of nuclear division in the rusts.

With the completion of the conjugate nuclear division, the fusion cell divides and the apical one-third, containing two daughter nuclei from separate spindles, is cut off (figs. 8, 14). This cell, the so-called aecidiospore mother cell, or, as it should more properly be termed, the aecidiospore initial cell, redivides soon afterward, producing the aecidiospore and the small intercalary cell. The basal cell meanwhile elongates and repeats the process of nuclear and cell division. Fig. 8 shows a distinctly two-legged basal cell of *P. Claytoniata*. Both the basal cell and the aecidiospore initial cell are four-nucleated as the result of conjugate division. The subsequent divisions of the basal cell and aecidiospore initial cell produce a catenulate series of alternating aecidiospores and intercalary cells.

The terms "fusion cell" and "basal cell" are not synonymous as I have used them. The fusion cell is the immediate product of the sexual cell fusion and may or may not function as a basal cell. It becomes a basal cell with the production of aecidiospores. The basal cell is a conidiophore ("basidium" of the earlier writers) from which the spores are abstricted. The term "basal cell" may with

this understanding be used with reference to the conidiophore of any of the spore forms found in the rusts, while the term "fusion cell" should be restricted to indicate the cell in which the transition from the uninucleated to the binucleated condition occurs.

In addition to the normal cell fusions between two gametes a number of cases of triple cell fusions were found. Two of these are illustrated in figs. 7 and 18. Fig. 7 is of *P. Claytoniata* and fig. 18 of *Ur. Caladii*. In both of these cases the three fusing cells lie in separate hyphae. In one or two other cases found two of the gametes came from the same hypha. Similar cases have also been found in *Mel. Lini* (**12**, fig. 18). The trinucleated fusion cells resulting from a fusion of three cells may function as basal cells. In this case the three nuclei divide simultaneously (figs. 12, 13), in the same manner as those in the binucleated fusion cells, and trinucleated aecidiospores and intercalary cells are formed. In fig. 9 a trinucleated aecidiospore initial cell has been abstricted from a trinucleated basal cell. The basal cell appears two-legged, but it is probable that one of the legs has been cut off in the section. Mature trinucleated aecidiospores are quite common in *P. Claytoniata;* several are often found in one section of a mature cup. They are somewhat less common in *Ur. Caladii* and *P. Violae* and are only rarely met with in the other forms.

Quadrinucleated aecidiospores were also found, but in fewer numbers than the trinucleated ones. A chain of quadrinucleated cells is shown in fig. 14. The apical aecidiospore of the chain contains 4 nuclei, while none are visible in the intercalary cell below it. Only 3 nuclei appear in the next aecidiospore, but the subtending intercalary cell is distinctly quadrinucleated. The lowest cell of the chain is probably an undivided aecidiospore initial cell. The 4 nuclei are arranged serially in the long axis of the cell. The chain was cut off at this point in the section and could not be located in adjoining sections. While no four-cell fusions nor four-legged basal cells were found, there can be little doubt that these occur in the cupulate aecidia as well as in the caeoma of *Mel. Lini* (**12**).

Many of the fusion cells formed undoubtedly do not function as basal cells for lack of space. Those in the upper part of the gametic tissue, immediately beneath the pseudoparenchyma, are more favor-

ably located for spore-production than those that lie more deeply in the tissue. The elongation of the fusion cell formed at the surface of the tissue is unimpeded except for the slight resistance offered by the empty, thin-walled cells of the pseudoparenchyma, while the fusion cell formed below must force its way between the closely packed gametes and fusion cells above. Sometimes they are able to do so and function as basal cells, but many were found that were apparently inhibited from so functioning by the resistance of the overlying cells.

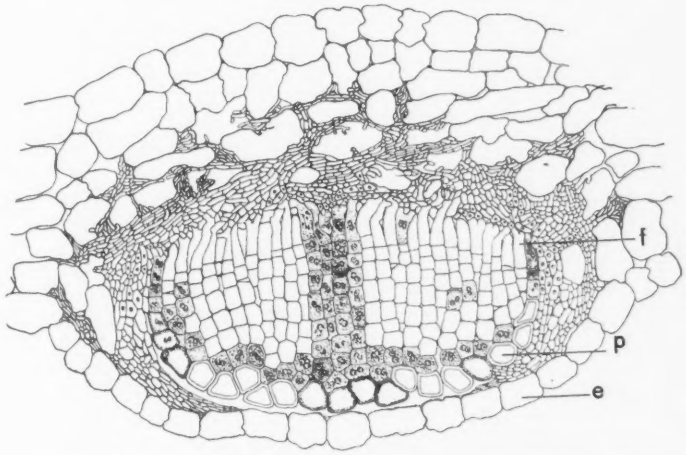

FIG. 5.—A mature aecidium of *Ur. Caladii* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

The fertile layer is deeply concave in *P. Claytoniata* and *P. Violae*, and extends about halfway up the lateral surfaces of the cup. The basal cells are more or less uneven in height, and the surface of the layer in outline has an irregular, broken appearance. The fertile layers of *Ur. Caladii* (text fig. 5) and of *P. Eatoniae* (text fig. 6) are especially broad and only slightly concave. The fertile layers of *P. Hydrocotyles* (text fig. 7) and of *P. angustata* are narrow and only slightly concave. The production of spore chains is confined to the basal surface of the cup and does not occur on the lateral surfaces. The basal cells of *P. Hydrocotyles* (text fig. 7)

form quite an even palisade and their bases converge toward a central point below. This conveys the impression that they may have arisen from a common central point or area.

Spore-production follows very rapidly after the fusions. The first spores formed are from the basal cells at the center of the fertile layer in the region where the first fusions occurred. The wave of spore-production proceeds from this center toward the borders of the fertile layer and follows closely after the fusion wave. The

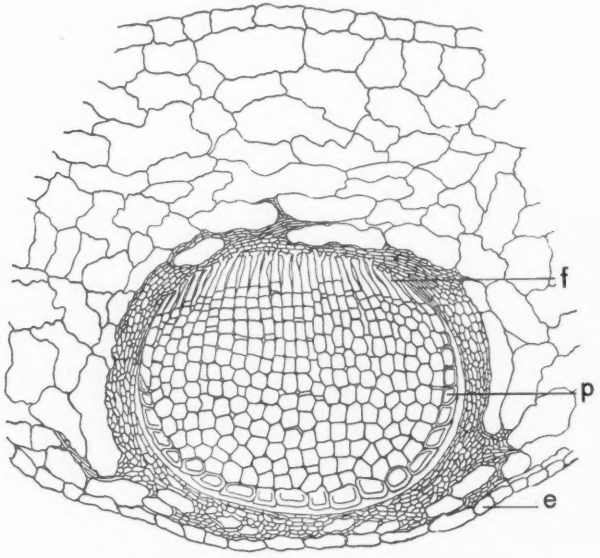

FIG. 6.—A mature aecidium of *P. Eatoniae* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

central basal cells continue to cut off spores and have usually produced a chain of 3 or 4 when the first spores are being produced from the basal cells on the extreme lateral margins of the fertile layer. The number of spores found in any one chain at this stage is dependent on the position of the basal cell with reference to the center of the fertile layer. The number decreases gradually from 3 or 4 at the center to one at the lateral margins. The surface of the spore mass is thus dome-shaped, with the highest point of the

dome at the center. It is convex in vertical section, while the surface of the fertile layer is concave. The mass of spores forms an ellipse, the long axis of which is parallel to the epidermis.

The production of spores now proceeds at a uniform rate across the entire extent of the fertile layer, and the dome-shaped roof of the spore mass is elevated or pushed toward the epidermis. The

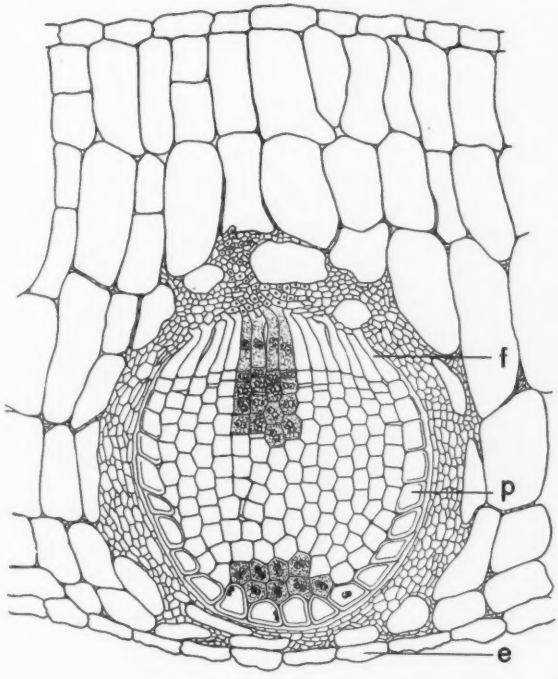

FIG. 7.—A mature aecidium of *P. Hydrocotyles* before the rupture of the epidermis: *e*, lower epidermis; *f*, fertile layer; *p*, peridium.

thin-walled, empty cells of the pseudoparenchyma apparently offer but little resistance. They are crushed and pushed upward or to one side, and either disappear entirely or remain as a thin layer of material without cellular structure. Meanwhile the leaf epidermis has been pushed up as an arch over the developing spore mass, as the result of the pressure, and when the pseudoparenchyma has

been entirely pushed away and the top of the spore mass presses directly on the epidermis, the arch is ruptured at the center.

Development of the peridium

The peridial cells make their appearance with the enlargement of the spore mass. The first peridial cells are seen at the apex of the dome-shaped spore mass, and are first distinguishable from the aecidiospores when the central spore chains are about 5 or 6 spores in length (text fig. 8). These first-formed peridial cells are produced by a metamorphosis of the apical aecidiospores of the central chains that involves an enlargement of the aecidiospore in all

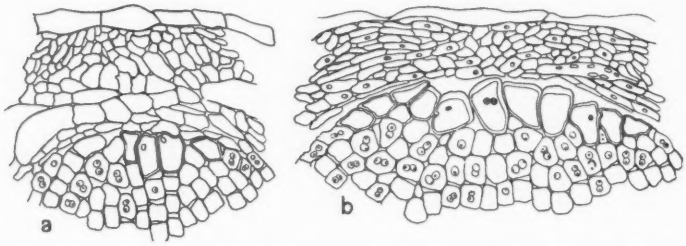

FIG. 8.—*a*, early stage in the formation of the peridium of *P. Claytoniata;* 4 peridial cells have been differentiated, all of which are apical cells of interior spore chains; *b*, a more completely formed peridium; 11 peridial cells are shown, 7 of which are from interior chains, and 4 (3 on the left and 1 on the right) are from the peripheral chains.

dimensions, a decrease in the density of its cytoplasm, and a marked thickening of its walls. The diameter of the mature peridial cell is about one and one-third times that of the mature aecidiospore, or more. The length of the cell is greater than the breadth, and its long axis is parallel to the axis of growth of the spore chain in which it is borne. This feature of the peridial cells is of some value in determining their point of origin, as will be seen later.

An early stage in the development of the peridium of *P. Claytoniata* is shown in text fig. 8, *a*. Only 4 peridial cells have been differentiated in this section. The walls of these are drawn with a double line. Three of them are apical cells of central spore chains, and the fourth is the apical cell of the fourth chain from the right-

hand border. The extreme outer border chains have as yet produced no peridial cells, and it is evident that the 4 peridial cells shown in the figure could not have been produced by them. The figure shows, further, that not all of the interior spore chains produce peridial cells, since the apices of some of these do not reach to the outer surface of the spore mass. A more complete peridium at a later stage is shown in text fig. 8, *b*. Eleven peridial cells appear in this section; 7 of these have apparently been borne on interior chains, although their connection with any one chain cannot be determined with certainty. The long axes of these cells are perpendicular to the epidermis and parallel to the axis of growth of the interior chains. The other 4 peridial cells, 3 on the left and 1 on the right, are evidently borne in the peripheral chains. It is also evident from this figure that not all of the interior chains have produced peridial cells, since there are 20 interior chains and but 7 peridial cells of interior origin.

While the peridial cell is forming, its connection with the spore chain on which it is borne is evident (text fig. 8), but with its enlargement at maturity and the changes in its position brought about by the continued elevation of the spore mass, this connection is made difficult or impossible to determine.

Not all of the peridium is formed from sterilized apical aecidiospores; its lateral walls are made up of the entire peripheral spore chains (text fig. 8, *b*). The cells of these chains are distinguishable as peridial cells when they have become the third or fourth cell from the base of the chain. The cells that make up the lateral walls of the peridium are differentiable from those that form the central arch in that they are modified aecidiospore initial cells rather than aecidiospores. They do not, except perhaps in rare cases, produce intercalary cells. Both the cytokinesis and karyokinesis of these cells are apparently inhibited by the same agent that produces the metamorphosis of the cell.

The production of peridial cells proceeds from the central point of the apical surface of the spore mass outward in all directions until a complete layer is formed over the entire apical and lateral surfaces of the spore mass. The peridium of this type of aecidium is normally but one cell in thickness. It is interesting to note,

however, that two or more layers of peridial cells are apparently formed regularly in certain species of *Peridermium* (3). When the peridium is completed over the entire outer surface of the spore mass, its subsequent enlargement is accomplished entirely by the basipetal addition of cells to its lateral walls from the peripheral basal cells.

The cytoplasm of the mature peridial cell is vacuolate and the nuclei are smaller and more compact than those of the aecidiospore. It is difficult to be sure whether they have decreased in size with the metamorphosis of the cell or whether they have not been completely reconstructed from the preceding mitosis. The latter explanation seems more probable and is supported by some observations that are not, however, conclusive. In size and general appearance they resemble the nuclei of the intercalary cells. They do not become disorganized; the chromatin masses and nucleoles stain deeply and are sharp and clean-cut. The walls stain with the orange, and a properly stained peridial cell is easily distinguished from an aecidiospore by the thickness of the wall as well as by the comparative emptiness of the cell and smallness of the nuclei. The outer side of the wall, the one next the pseudoparenchyma, is thicker than the inner or lateral sides (fig. 15). This was true to some extent of all of the forms I have studied. The nuclei are often located near the thickest part of the wall. The process of wall-thickening accompanies the decrease in the density of the cytoplasm, and the natural assumption is that the thickening is produced by the deposition of substances from the cytoplasm. No stratification appears in the walls. They may be variously sculptured, however, and the outer portion of the wall is usually marked by transverse striae.

The origin of the peridium is more easily followed in the broad cup of *Ur. Caladii* than in any of the other forms. The greater part of the peridium that is formed here before the rupture of the epidermis originates from interior spore chains. This is apparent even in mature cups, as shown in text fig. 5, which is a semi-diagrammatic representation of a stage before the rupture of the epidermis. Of the peridial cells shown here, 14 are in all probability of interior chain origin. There are about 29 interior chains.

It seems that in general the shape of the cup and the breadth of the hymenium determine the relative numbers of peridial cells of peripheral and interior origin. If the cup is shallow and the fertile layer broad, as in *Ur. Caladii*, the number of those of interior origin will be comparatively greater than when the cup is deep-seated and spherical and the fertile layer narrow, as in *P. Hydrocotyles* (text fig. 7).

So far as I am aware, no estimate of the approximate number of spores produced in an aecidium cup has been made. A comparatively accurate estimate of the number produced in the aecidium of *P. Eatoniae* was made as follows: The spore chains in median sections of 10 mature aecidia were counted. The average number found was 32. Since the cup is circular in cross-section, its radius would be 16 and the area of the cross-section 804.24. The average number of spores per chain (10), multiplied by the number of spore chains (804.24), gives a total production of 8042 spores. The estimate of 10 spores per chain is low, since the count was necessarily made before the opening of the cup, and the production of spores probably goes on for some time after this.

Wolf (**29**) has recently called attention to the production of internal aecidia of *P. angustata* on *Lycopus virginicus*. These were found principally in sections of stems and petioles. The cups are very deep-seated, and being unable to reach the epidermis discharge their spores into the parenchyma or the pith cavity. No internal aecidia appear in any of my sections of this species, as they are all of leaf tissue. I have found cases of internal spermogonia, however, in *P. Claytoniata*. These were buried at considerable depth in the parenchyma of the stem, but were normal in other respects. The spermatia had been discharged in some cases and were found in the intercellular spaces above the ostiole. Still more curious were several cases of intimate association between spermogonia and aecidia in which the spermogonium was borne in the center of an aecidium. None of the aecidia in these cases had reached the stage of sporulation, but the spermogonia had produced spermatia in abundance. The condition is evidently abnormal, but could have been construed as proof of a sexual relation between the spermogonium and aecidium by the older exponents of this view. It does

show the similar and perhaps interchangeable nature of the mycelia that produce the two fructifications.

Discussion

From the evidence gained from the study of the 6 species of aecidia treated here, the conclusion is reached that the essential processes involved in the development of the cup and caeoma types of aecidia are similar. The gametes of the two are apparently similar in origin. They are borne, in both types of sori, in perpendicular hyphae, but those of the cup are less markedly differentiated in size from the surrounding cells than those of the caeoma. Fertilization is accomplished in the cup, as in the caeoma, by complete cytoplasmic union between two morphologically equivalent gametes and produces a double, binucleated cell that later functions as the basal cell for a chain of aecidiospores. The fertile layer of both types enlarges by centrifugal growth, the first fusions occurring at the center of the gametic tissue and the last ones at the lateral margins. The breadth of the fertile layer of the cup is determinate, being limited by the breadth of the primordium and the layers of encircling hyphae on the lateral surfaces, while that of the caeoma is somewhat indeterminate, the only apparent limiting factor being the food supply.

The development of a peridium in the cup is the only sharply distinctive feature that separates the two types of aecidia. The peridium is formed as an outer layer of sterilized, differentiated cells that covers and presumably protects the spores beneath. The origin and growth of the peridium were found to conform in all essentials to RICHARDS' descriptions (**27**). It is composed of metamorphosed aecidiospores and aecidiospore initial cells that are not differentiable from the others, before their metamorphosis, except by their position on the periphery of the spore mass. The central part of the arch of the peridium is formed from the modified apical aecidiospores of the interior spore chains, while the lateral walls are formed from the undivided aecidiospore initial cells of the peripheral chains. The peridium, like the fertile layer, enlarges centrifugally. The cells at the center of the arch are first differentiated and the differentiation proceeds from this point outward in all directions

until a complete layer is formed over the entire mass. The subsequent enlargement of the peridium is accomplished by the basipetal growth of the lateral chains of peridium initial cells.

The "buffer" cells of the caeoma are homologous with the pseudoparenchyma cells of the cup, and represent a scanty production of pseudoparenchyma. The production of a peridium seems to be dependent on the presence of a considerable pseudoparenchyma, and this is in turn the result of the deep location of the primordium in the host tissue, and the deep location of the gametes in the primordium.

As I have elsewhere stated (**12**), in the caeoma of *Mel. Lini* the gametophoric hyphae are 3 or 4 cells long. Two sterile cells are normally produced, and though, as a rule, but one gamete is formed in each hypha, two are occasionally found. In the production of more than one sterile cell and the tendency to produce more than one gamete there is seemingly a transition toward the conditions found in the cup. The cup of *Ur. Caladii*, as found on *Arisaema*, is very much like a caeoma in appearance before the formation of the peridium. The gametophoric hyphae are 6 or 7 cells in length, and 4 or 5 of the apical cells are sterilized. If, as I have suggested, the production of a peridium is correlated with the amount of pseudoparenchyma produced, the line of separation between the aecidia without and those with a peridium should be found at some point between the caeoma of *Mel. Lini* with 2 sterile cells, and the cup of *Ur. Caladii* with 4 or 5. A careful study of the more deeply seated caeomas may perhaps reveal a more or less marked differentiation of the outermost spore layer. Those species of cupulate aecidia with evanescent peridia are perhaps most nearly like the deep caeomas.

The study of the origin of the peridium that is found in the uredosorus of certain genera should prove of considerable interest, but apparently no such study has ever been made and no data are available. According to ARTHUR'S treatment of the Uredinales in the *North American flora* (**2**), 6 genera of the family Uredinaceae have uredosori with peridia: *Pucciniastrum*, *Melampsoridium*, *Hyalopsora*, *Uredinopsis*, *Melampsoropsis*, and *Cronartium*. *Melampsoropsis* has catenulate uredospores, while

those of the remaining 5 genera are reported as pedicellate. A peridium of the type found in the aecidium cup is to be expected in a deep-seated uredosorus of catenulate spores, but is scarcely to be looked for in a sorus of pedicellate spores, where the supposed protective function is normally performed by paraphyses.

No central organs ("fertile hyphae") or multinucleated cells were found in any of the species of aecidia studied, and it is therefore concluded that these do not necessarily occur in aecidia of the cup type. While this by no means precludes the production of multinucleated cells in other species, it is evidence that these are not necessary for the development of the centralized structure of the cup. It is perhaps possible that the multinucleated cells found by OLIVE in certain cupulate aecidia are the result of multiple cell fusions. The presence of tricellular fusions and trinucleated and quadrinucleated aecidiospores in several of the species I have studied shows that pluricellular fusions are rather common in the cup as well as in the caeoma.

The aecidium cup, from the evidence presented here, is not to be regarded as an organ with a centralized development like that of the ascocarp, as DEBARY and others have considered it, but is seen to be merely a remarkably unified colony of individual gametophores. The presence of a central organ is no more necessary to the development of the cup than the caeoma. The existence of uredosori with catenulate spores, that arise from sporophytic mycelium and hence cannot be considered the product of central organs, is further evidence that a seemingly centralized fructification may be developed from a colony.

The presence of trinucleated spores in various rust sori has been noted by a number of investigators, and there seems to be no question that such spores, when found in the aecidium or the teleutosorus of the micro-forms, are the products of tricellular fusions. The germination of a trinucleated spore would be highly interesting to observe. HOFFMAN believes that one of the nuclei in trinucleated spores of *Endophyllum Sempervivi* degenerates, but has no convincing proof of this.

As previously noted, branching basal cells have been found in the aecidium of *P. Falcariae* by DITTSCHLAG and in the sorus of

Endo. Sempervivi by HOFFMAN. Although I have found no such cells in any of the aecidia included in this study, I have found a single case of a basal cell that seems to have given rise to a branch in the aecidium of *Aecidium Dicentrae* Trel. Only a few sections of this form have been examined, and hence no estimate can be made as to the prevalence of the condition. In the single case seen, the second basal cell seems to have arisen as a lateral branch of the primary basal cell, and the opening between the two has not been closed by wall-formation. Both basal cells have produced a chain of spores.

HOFFMAN compares these branching basal cells to the basal cell of the primary uredosorus as described by CHRISTMAN. The two cases, however, are not at all comparable. The basal cell of the primary uredosorus gives rise to successive stalked spores that originate as buds on the upper surface of the cell. The comparison is made, therefore, between a bud that produces a stalked spore in one case and a basal cell in the other. As CHRISTMAN has pointed out, the homology lies between the primary uredospore and stalk cell and the aecidiospore and intercalary cell. The homology is also extended to include the basal cells of the two sori.

According to CHRISTMAN, the basal cell is the true morphological unit, and the basal cells of the different sori are to be considered as homologous. This, however, involves the difficulty, which CHRISTMAN recognized, that the basal cells of the uredosorus and teleutosorus are not the outgrowth of fusion cells, as are those of the primary uredo and aecidium, but are borne on a mycelium of binucleated cells. The basal cell of the micro-forms is also without doubt to be homologized with that of the aecidium, since OLIVE's work on *P. transformans* and that of WERTH and LUDWIGS on *P. Malvacearum* indicate that the basal cell of these forms is the outgrowth of a fusion cell.

The evident homology between the primary uredospore and the aecidiospore is used by CHRISTMAN as a strong argument that the eu-type of rust with catenulate aecidiospores cannot be considered as a primitive type, but is rather a highly specialized and derived type. If the homology is to be accepted, and it seems to have been very generally, the catenulate method of aecidiospore-production

must have been derived from the pedicellate, and the primary uredo is therefore more primitive than the aecidium. For, as he argues, the intercalary cell is thus seen to be in reality a stalk cell that has been necessarily shortened by the catenulate method of spore-production and persists as a vestigial cell. If the aecidium, however, is considered the primitive sorus and the uredo the derived form, the intercalary cell must be considered a functionless structure that persists and is later modified into a structure of value to the organism in the stalk of the uredospore.

In view of this convincing explanation of the nature of the intercalary cell, one can scarcely agree with GROVE (13) that *Endo. Sempervivi* is to be considered as a representative of the primitive type of rusts. The fact that the spores of this species are borne in a complex aecidium-like fructification, surrounded by a peridium and accompanied by intercalary cells, makes its acceptance as a primitive type extremely difficult. To all morphological appearances the spores are aecidiospores and the sorus an aecidium. The spores, however, function as teleutospores, as HOFFMAN has conclusively shown. GROVE'S acceptance of *Endophyllum* as a primitive type and his relegation of the micro-forms to the position of reduced types seem inconsistent when the relative complexity of the two types of sori are considered. It certainly seems more logical to consider *Endophyllum* a reduced form, as the gametophytic generation of a former eu-heteroecious or autoecious species that has dropped the uredo and teleuto stages, with the assumption of a teleutosporic method of germination by the aecidiospore, and to regard the micro-forms as the more primitive and ancestral. The assumption of the teleutosporic method of germination by an aecidiospore is not a difficult conception, since nothing more than the fusion of nuclei in the spore should be necessary for its accomplishment.

It is interesting to note that KUNKEL (17) has recently discovered a companion form to *Endo. Sempervivi* in the common orange rust of the blackberry, *Caeoma nitens*. The life history of the two species is practically identical, seemingly, but the sorus of the latter is a caeoma, while that of the former is an aecidium cup. *Caeoma nitens*, therefore, should offer a much better ancestral type for

GROVE's argument than *Endo. Sempervivi* because of the relative simplicity of the sorus, but the presence of intercalary cells, on the other hand, is a strong argument against its acceptance as such.

GROVE advances the perennial nature of the mycelium of *Endo. Sempervivi* as further proof of the primitive nature of the fungus. The perennial nature of the mycelium seems to me, however, a highly specialized condition. A more desirable relation from the standpoint of the continued welfare of the fungus is difficult to conceive. The fungus thus becomes independent of the chance association of hosts for its propagation. A decrease in the number of spore forms is perhaps to be expected with the increased efficiency of the perennial mode of life. The necessity for the production of resting spores is done away with, as well as the production of repeating spores for extensive propagation. A perennial mycelium is also found in certain of the short-cycled micro-forms, for example *P. fusca* and *P. Adoxae*, and it seems, therefore, that this condition cannot be advanced as proof of either a primitive or a derived condition. The efficiency of the perennial gametophytic mycelium may be one reason why the gametophyte has maintained the supremacy and these micro-forms have persisted as such.

The remarkable cases of correlation between the teleutospores of certain micro-forms and those of certain eu-heteroecious forms that have been cited by FISHER (11) and others are certainly strong evidence of a phylogenetic relation between the two groups. Further study of this phase of rust morphology will doubtless bring to light many groups of correlated species with life cycles of various lengths, and will in all probability settle many of the problems as to the origin and development of such types. The most reasonable view of the phylogeny of the rusts seems to me that of DIETEL as amplified by CHRISTMAN and OLIVE. This view regards the micro-forms as the most primitive forms, from which the brachy-, opsis-, and eu-forms have been derived by the lengthening of the sporophyte generation and the intercalation of aecidiospores and uredospores.

This work was conducted under the direction of Professor R. A. HARPER, to whom I am indebted for many helpful suggestions and criticisms.

Summary

1. The essential features in the development of the cup are similar to those found in the development of the caeoma. The initial hyphal mass, or primordium, is formed by hyphae growing radially toward the center of the future cup.

2. The cup is more deeply seated and produces a greater number of sterile cells and gametes to each gametophoric hypha. The gametes form a fertile layer two or more cells in thickness. The sterile cells that form the pseudoparenchyma of the cup are homologous with the "buffer" cells of the caeoma.

3. Sexual cell fusions, by the breaking down of the cell walls between two equal gametes, were found in 6 additional species of cupulate aecidia, namely *Ur. Caladii*, *P. Claytoniata*, *P. Violae*, *P. Hydrocotyles*, *P. Eatoniae*, and *P. angustata*. Although the actual fusion stages were not seen in the last named species, the presence of two-legged basal cells is evidence that the fusions are of the same type as those found in the other species. No central organs ("fertile hyphae") or multinucleated cells were found. The organization of the cup, therefore, is merely that of a remarkably unified colony of gametophores.

4. Triple cell fusions were observed in *P. Claytoniata* and *P. Violae*, and trinucleated aecidiospores were frequently found in both of these species and in *Ur. Caladii*. Several quadrinucleated aecidiospores and a chain of quadrinucleated cells were found in *P. Claytoniata*.

5. The first fusion cells are formed at the center of the gametic tissue, and the subsequent ones are formed on all sides of this center in centrifugal order, until the lateral borders of the aecidium are reached.

6. The fusing cells may have their long axes in general in the long axis of the cup, for example *P. Claytoniata*, *P. Violae*, *P. Hydrocotyles*, and *Ur. Caladii*, or tangential to its curved basal surface, for example *P. Eatoniae*.

7. The presence or absence of a peridium is a natural but not very fundamental distinction between the aecidium cup and the caeoma. The production of a peridium is correlated with the deep location of the cup and the extensive formation of sterile cells.

8. As has long been known, the peridial cells are metamorphosed aecidiospores and aecidiospore initial cells. The central arch of the peridium is formed from the apical aecidiospores of the interior spore chains and the lateral walls from entire peripheral spore chains. The first peridial cells are produced at the center of the arch and the peridium enlarges from this point centrifugally until the bases of the lateral walls are reached. Its subsequent enlargement is by the basipetal growth and sterilization of the peripheral spore chains.

COLUMBIA UNIVERSITY

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EXPLANATION OF PLATES I AND II

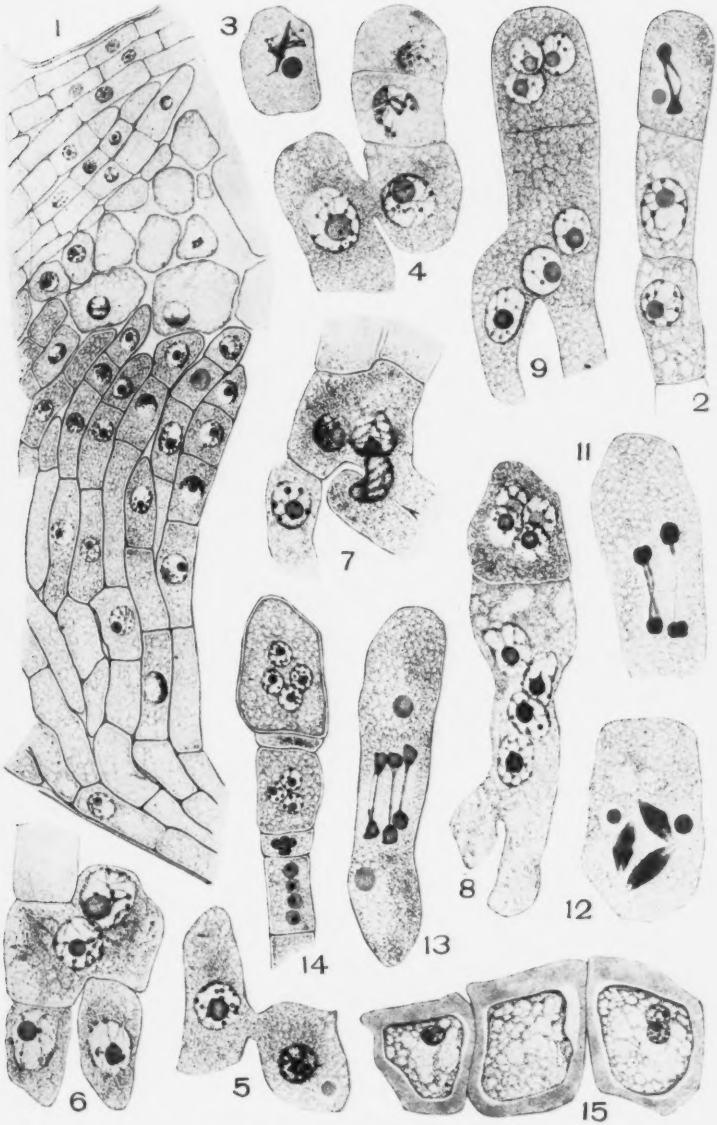
All of the figures were drawn with the aid of the camera lucida, and, except where otherwise mentioned, at a magnification of 1140 diameters. They are all placed in their natural position in the sorus, with the top of the page representing the direction of the leaf epidermis.

Puccinia Claytoniata

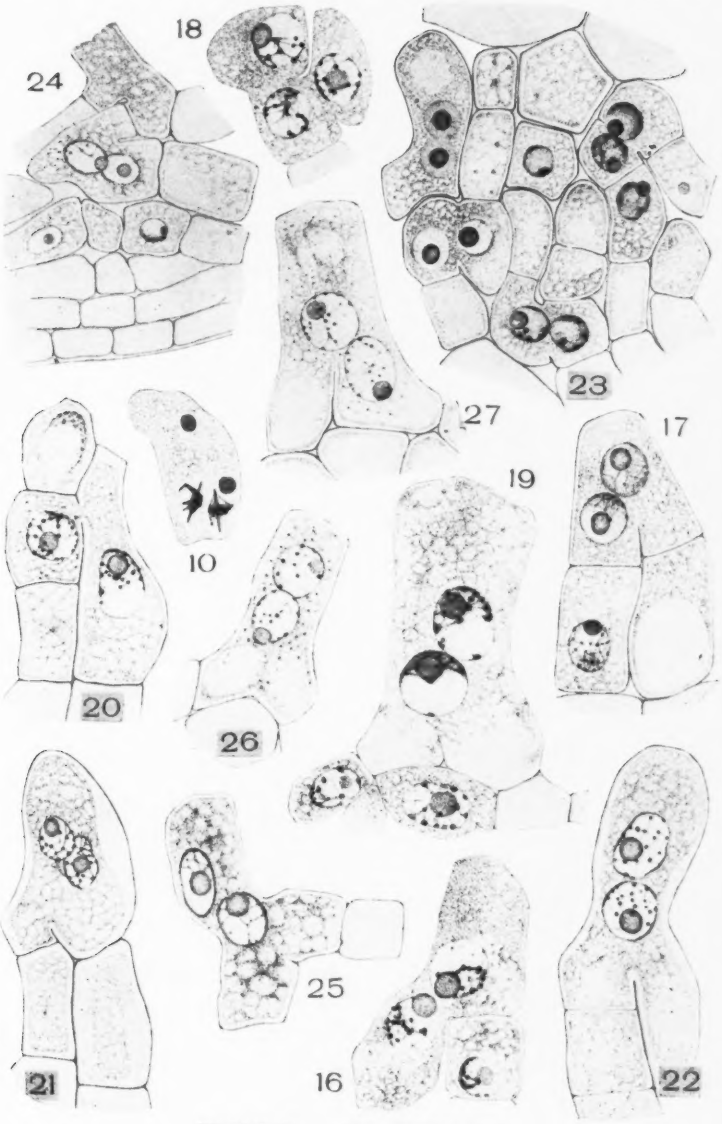
FIG. 1.—A section through the lateral border of the cup before the cell fusions; 6 layers of encircling hyphae are seen at the top, below these are the sterile cells of the pseudoparenchyma and below these the perpendicular gametophoric hyphae; all of the cells are uninucleated; ×570.

FIG. 2.—A more highly magnified view of the tip of a gametophoric hypha in a young aecidium; the nucleus of the apical cell is shown in the anaphase of mitosis.

FIG. 3.—An earlier stage of mitosis in a uninucleated cell.



FROMME on AECIDIUM CUP



FROMME on AECIDIUM CUP

FIGS. 4 and 5.—Two early stages of cell fusions.

FIG. 6.—A completed cell fusion.

FIG. 7.—A tricellular fusion.

FIG. 8.—A two-legged basal cell and above it an aecidiospore initial cell; 4 nuclei are found in both cells as the result of the preceding conjugate divisions; ×900.

FIG. 9.—A trinucleated basal cell and aecidiospore initial cell.

FIG. 10.—Early stage of conjugate mitosis in an aecidiospore initial cell.

FIG. 11.—Anaphase of conjugate mitosis in a fusion cell.

FIG. 12.—Simultaneous division of three nuclei in a fusion cell.

FIG. 13.—A later stage than the preceding; the elongated spindles lie parallel with each other and the long axis of the fusion cell.

FIG. 14.—A chain of quadrinucleated aecidiospores and intercalary cells; ×570.

FIG. 15.—Three peridial cells from the central region of the peridium; ×570.

Uromyces Caladii

FIGS. 16 and 17.—Two cases of completed cell fusions.

FIG. 18.—A tricellular fusion.

FIG. 19.—A two-legged basal cell.

Puccinia Violae

FIG. 20.—A very early stage of cell fusion in which the fusion pore is still very small.

FIG. 21.—A completed cell fusion.

FIG. 22.—A two-legged fusion cell.

Puccinia Hydrocotyles

FIG. 23.—Three cases of cell fusion within a small area; the borders of two cells of the pseudoparenchyma are shown at the top of the figure.

Puccinia Eatoniae

FIG. 24.—Fusion between two cells in horizontal lying hyphae near the base of the sorus; the base of a two-legged fusion cell lies just above the fusing gametes.

FIG. 25.—A two-legged fusion cell that has bent up at a sharp angle and elongated in the direction of the epidermis.

Puccinia angustata

FIGS. 26 and 27.—Two-legged basal cells.

INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

NO. 2. ANATOMICAL EVIDENCES OF REDUCTION IN CERTAIN OF THE AMENTIFERAE

IRVING W. BAILEY AND EDMUND W. SINNOTT

(WITH PLATES III–V AND THREE FIGURES)

The earlier taxonomists by systematic studies, principally of external characters, have contributed much toward a truly natural classification of the angiosperms, but the problem is such an intricate one that in searching for a satisfactory solution evidence from all fields of botanical research must be considered and harmonized.

In view of the assistance given by comparative anatomists in elucidating the phylogeny of gymnosperms and lower vascular plants, the recent hypothesis of Professor JEFFREY and his pupils, in regard to the development of "aggregate," "compound," and "multiseriate" rays in dicotyledonous angiosperms, merits careful consideration by taxonomists, since, if shown to rest on secure foundations, it is likely to produce radical changes in existing systems of classification.

The "aggregate" ray hypothesis

The salient features of this hypothesis may be summarized as follows: The angiosperms have not been derived from the Bennettitales, but from ancestors which possessed only linear or uniseriate rays, such as are a well developed feature of the Coniferales. During the warmer times of the Mesozoic, sheets of parenchymatous tissue were "built up" from congeries of uniseriate rays about the traces of leaves which persisted for a number of seasons. The influence at work in the development of this tissue was originally the demand for the storage of assimilates descending from the large leaves of these earlier angiosperms. These "foliar" rays have persisted in their very primitive "aggregate" condition (composed of congeries of small rays), and in their more advanced "compound" condition (completely parenchymatous), in primitive families of

the dicotyledons. With the advent of a severe winter season and the consequent acquirement of the deciduous habit in connection with the leaves, the organization of these storage systems about the leaf traces as permanent centers was no longer advantageous or desirable. Thus in the development of the "multiseriate" type of ray which characterizes the majority of living dicotyledons, the enlarged units of the aggregating mass of foliar ray tissue have been diffused more or less uniformly throughout the stem. Besides being less unwieldy, this system of smaller rays affords equally large capacity for storage and a more convenient general relation between conducting, supporting, and storage tissue.

The principal arguments in favor of this hypothesis were first formulated in a paper presented by JEFFREY ('09) before the Botanical Society of America at Baltimore.

> One of the most striking triumphs of modern plant anatomy is to have discovered many examples of recapitulationary confirmation of the principle of evolution. To take a modern and striking example, let us consider our common and flourishing northern genus, the oak. You are all familiar with the very broad rays which constitute so ornamental a feature of the structure of oak wood. You are likewise doubtless aware that the weight of paleobotanical evidence speaks for the derivation of the oaks from ancestors resembling the chestnuts, since the older oaks approach the chestnuts both in their foliage and in their reproductive organs. The wood of the chestnut differs, however, strikingly from that of oaks by the entire absence of large rays. It has been recently discovered that certain oaks of the gold gravels (Miocene-Tertiary) of California have their large rays composed of aggregations of smaller rays. In the seedlings of certain of our existing American oaks this condition, interestingly enough, is a passing phase, which by the loss of the separating fibers in the congeries of small rays produces the characteristic large rays of the adult. This condition of development in the living oaks is all the more significant because in certain breech-fertilized or chalazogamic amentiferous trees of the present epoch, such as the alder, the hazel, and the hornbeam, such aggregated, so-called false, rays are a permanent feature of structure in the adult. From the anatomical side, in the case of the lower Amentiferae, we have accordingly at the same time an interesting example of the general law of recapitulation and a confirmation of the view expressed by TREUB and NAWASCHIN, on evidence from the gametophytic and reproductive side, that the breech-fertilized Amentiferae are relatively primitive angiosperms.

The arguments blocked out in this paper have been elaborated under JEFFREY'S direction by several students (see bibliography).

Especially significant are two collateral lines of evidence which have played an important part in amplifying the original hypothesis. The first of these is concerned with the connection between certain "aggregate" and "compound" rays and the traces of leaves, a phenomenon which is said to indicate conclusively that "aggregate" and "compound" rays were "built up" for purposes of storing the assimilates descending from the large persistent leaves of mesozoic angiosperms. The second line of evidence deals with the apparent disintegration of "foliar" rays in passing from the first formed to the mature portions of the stems of certain Ericales, Fagales, and Casuarinaceae. This ontogenetic sequence has been interpreted as indicating that the "multiseriate" type of ray originated from the diffused portions of "aggregate" or "compound" rays.

Objections to the "aggregate" ray hypothesis

In endeavoring to trace certain steps of the evolutionary history of the so-called "aggregate" and "compound" rays in the Fagales, one of the writers (BAILEY '11) discovered indications of reduction in *Castanea* and *Alnus*. Additional investigations ('12) of these genera, and of *Castanopsis*, *Ostrya*, and *Carpinus* revealed much evidence for believing that the "aggregate" and "compound" rays have disappeared or are in the process of disappearing from living species of these genera. Furthermore, GROOM ('11) has suggested that the small rays of *Quercus* may have originated by the disintegration of primitive wide multiseriate rays. It is somewhat difficult to harmonize completely these observations with the general trend of the investigations upon "wide" rays, since they introduce the possibility that the congeries of small rays (the so-called "aggregate" rays) may be in every case stages in the "breaking down" rather than in the "building up" of wide rays. This fact is particularly significant when we consider that the "aggregate" ray hypothesis derives much of its support from the theory that the chalazogamic Amentiferae are in all probability the most primitive living angiosperms, for many botanists, from comparative studies of sporophytes and gametophytes, consider that these angiosperms with unisexual flowers are reduced rather than truly primitive.

The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for the determination of the position of plants in a phylogenetic sequence. The paleontological evidence which has been cited cannot be considered to be entirely convincing, since "multiseriate" rays are found in middle and upper cretaceous dicotyledons, although according to the "aggregate" ray hypothesis they are the most recent development of the angiosperm ray. If "aggregate" and "compound" rays originated for purposes of storing the assimilates descending from the persistent leaves of mesozoic angiosperms, and were later replaced by "multiseriate" rays as an adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit by the leaves, we should hardly expect to find the "multiseriate" ray well developed in cretaceous angiosperms or in families which have lived in moist, warm, tropical conditions since ancient times. It is a notable fact, therefore, that "multiseriate" rays are characteristic of such typically tropical families as the Lauraceae, Anonaceae, Ebenaceae, Rubiaceae, Myristicaceae, Apocynaceae, Myrtaceae, etc., although there is no evidence to show that these families have been exposed to a refrigerated climate since the Mesozoic. On the other hand, the "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae and the temperate families Betulaceae, Fagaceae, and Ericaceae. Apparently, therefore, the most conclusive evidence that has been advanced in favor of the origin of the "aggregate" and, *pari passu*, of the "compound" and "multiseriate" rays must be considered to be that derived from the study of the phenomena of recapitulation.

STRUCTURE OF SEEDLINGS

We have noted above that JEFFREY places much emphasis upon the fact that the first formed rays of seedling oaks are all of the uniseriate type that occur throughout the wood of the supposedly very primitive chestnut. In white oaks with deciduous foliage (subgenus *Lepidobalanus*) this primitive condition persists until the plants have attained considerable size. These oaks, therefore, are assumed to be more primitive than oaks of the

subgenus *Erythrobalanus*, since in the latter the "aggregation" and "fusion" of rays begins much earlier. Similarly, the "live" or "evergreen" oaks are regarded as more primitive than either of these types, since they possess even in the mature wood "aggregate" tissue from which the separating fibers have not been entirely eliminated.

The writers have recently examined seedlings of different species of the Fagales, and have found phenomena that are apparently of considerable interest. Especially significant are the effects of different degrees of vigor upon the development of ray structures in seedling plants. Suppressed, slow-growing, feeble plants are characterized in many cases by the retarded development of large rays. In fact, the effect of stunted growth may be so strongly marked that only uniseriate rays are formed in stems 30–50 years old. On the other hand, in plants with large, vigorous, well nourished growing points the development of large rays is often accelerated. Vigorous specimens of certain oaks, e.g., *Quercus rubra* L., may even possess wide rays (so-called compound or completely parenchymatous rays) in the first formed portion of the seedling stem (figs. 3 and 13). In the ontogeny of these rays, as in those of *Fagus grandifolia* Ehrh. and *F. sylvatica* L. (fig. 1), there are no putative stages of "aggregation" and fusion.

It is somewhat difficult to explain satisfactorily the facts of seedling anatomy in the Fagaceae, since a strict application of the doctrine of recapitulation might be considered to indicate in the case of certain seedlings that the multiseriate type of ray is primitive, whereas in other young plants it seems to show that wide rays have been "built up" phylogenetically from congeries of uniseriate rays.

The seedling or young plant has been shown in a number of cases to retain characters that are in all probability ancestral, but these phenomena have been interpreted differently by different investigators. HILL and DEFRAINE and others maintain that the seedling is very sensitive to changes in its internal or external environment and therefore of little or no value for phylogenetic purposes. Primitive structures persist only where they are of functional importance in the young plant. In opposition to this

are the views of JEFFREY, who considers that HAECKEL's doctrine of recapitulation is of "universal validity," as invariably operative as the laws of chemistry, physics, and the other cognate sciences. A more conservative working hypothesis which combines elements from each of these antagonistic extremes is held by other biologists, who believe that there are categories of predominantly conservative and of predominantly variable characters, just as there are organs or regions of the plant that are more retentive of primitive characters than others. The mere fact that certain ontogenetic characters have been found to be extremely inconstant and sensitive to physiological conditions does not necessarily invalidate the doctrine of recapitulation. Nor does the fact that the young plant has been shown in certain cases to retain ancestral features indicate that every seedling character is of phylogenetic value. The seedling may display a strong tendency toward conservatism and still be subject to environmental influences, just as the behavior of a falling body may be influenced by other forces than that of gravity. However, the fact that any character in the young plant may be subject to modification by physiological changes makes it difficult in many cases to distinguish palingenetic from cenogenetic features. Phylogenetic conclusions drawn from the study of the structure of seedlings are not conclusive unless substantiated by reliable corroborative evidence.

In view of the somewhat paradoxical behavior of wide rays in the seedling stem, the structure of other regions which are supposed to be conservative and retentive of ancestral characters has an important bearing on the problem under discussion.

THE ROOT

In a recent paper JEFFREY ('12) makes these comments upon the conservatism of the root:

> There are organs of the plant, for example, even more strongly retentive of ancestral characters than the seedling stem. Perhaps the most conservative organ is the root, which varies so little in its fundamental organization throughout the vascular plants that one formula will represent the organization of all roots.

The roots of *Fagus grandifolia* and *F. sylvatica* (fig. 2) possess even in the first formed secondary xylem multiseriate rays which

radiate from the clusters of protoxylem. These wide sheets of homogeneous ray parenchyma do not arise by a process of "compounding." Similarly, the "secondary" multiseriate rays which develop as the root increases in circumference are not formed by the "aggregation" and "fusion" of small rays, but originate, as they do in the young stem and mature shoots, by the widening of a single uniseriate ray. Conditions equally significant exist in other genera of the Fagales. For example, wide multiseriate rays occur in the first formed portions of the roots of *Quercus velutina* Lam., although in the seedling stem only uniseriate rays are formed by the first activity of the cambium. On the other hand, certain species of the Betulaceae and Fagaceae possess only uniseriate rays in the first formed portions of the roots, although so-called "aggregate" or "compound" rays may develop during subsequent growth (fig. 6). In the root, as in the seedling stem, variations in vigor and other physiological conditions produce marked variations in the development of rays. Vigor usually accelerates the formation of large rays and feeble or stunted growth tends to reduce their size or retard their development.

THE REPRODUCTIVE AXIS

SCOTT in his studies of cycads was the first to point out in a convincing manner the importance of the anatomy of the reproductive axis as a possible seat of conservatism. More recently JEFFREY, working upon the comparative anatomy of gymnosperms, has reached the conclusion that this region is even more retentive of ancestral characters than is the seedling stem.

The flowering axes of many dicotyledonous plants are less favorable for the study of structures which occur in the secondary wood than are the cone axes of gymnosperms, since they often are herbaceous or possess only a narrow zone of secondary tissue. It is fortunate, therefore, that the peduncles of many species of *Quercus* and *Casuarina* have wide zones of secondary wood and well developed rays. The peduncles of the red or black oaks (subgenus *Erythrobalanus*) are particularly interesting, since they persist through two growing seasons and possess in consequence two layers of secondary tissue. The development of ray structures

in these species is well illustrated by the peduncles of *Quercus coccinea* Moench. and *Q. ilicifolia* Wang. Multiseriate rays are formed by the first activity of the cambium and show no putative stages of "aggregation" and "fusion" in their ontogenetic development (fig. 15). Conditions equally significant have been observed by the writers in the peduncles of *Casuarina suberosa* Otto and Dietr., a species which possesses well developed "aggregate" rays in the seedling stem (fig. 7). The peduncles of *Quercus pedunculata* Ehrh., *Alnus maritima* (Marsh) Muhl., *A. incana* L. Moench., and *A. yasha* Matsum, are slender and possess narrower zones of secondary tissue. However, even in these peduncles biseriate and triseriate as well as uniseriate rays are often formed by the first activity of the cambium.

THE NODE

SCOTT, JEFFREY, and others have emphasized the conservatism of the leaf trace and neighboring tissues. The structure of the nodal region is therefore important in a discussion of the origin and development of "aggregate" and "compound" rays.

Throughout the Fagales there is a marked tendency for large rays to be more strongly developed in the young shoot in the vicinity of those strands of the vascular cylinder which are about to pass out to the leaves. These rays are in many cases composed of homogeneous ray parenchyma, whereas the wide rays in other radii of the stem arise apparently by a "compounding" process from congeries of uniseriate rays. Perhaps the most significant conditions are those which occur in supposedly primitive representatives of the Fagales. Among the Betulaceae, for example, vestiges of "aggregate" rays may occur in the nodal region when the internodes possess only uniseriate rays (fig. 12). Similar conditions are of frequent occurrence in the white oaks (subgenus *Lepidobalanus*). Stems of *Quercus alba* L. often possess for many years only uniseriate rays except in the vicinity of the lateral traces of the leaves (fig. 10). The root may likewise be devoid of wide sheets of ray tissue except in the vicinity of the vascular elements which pass out to the rootlets (figs. 6, 11, and 20). In this region vestiges of wide sheets of homogeneous ray parenchyma occur. Especially

significant are the wide multiseriate rays which radiate from the clusters of primary elements in the hypocotyledonary region of young plants of *Quercus virginiana* Mill., a "live" or "evergreen" oak which often possesses "aggregate" rays in the mature wood of the stem.

THE FIRST ANNUAL RING

The first elements formed by the cambium or lateral growing point (the so-called first annual ring) have been considered by JEFFREY, THOMSON, and others to be conservative of ancestral characters. It has been shown in the preceding pages that the first formed portions of the seedling stem and root may possess often only uniseriate rays which later appear to "aggregate" and form wide sheets of ray tissue (figs. 4 and 6). However, in certain cases the first annual ring of vigorous shoots and roots may possess "aggregate" and "multiseriate" rays when the mature portions of these organs develop only uniseriate rays. For example, vestiges of wide multiseriate rays have been observed in very vigorous young roots of *Castanea dentata* (Marsh) Borkh. (figs. 11 and 20). These rays occurred in the vicinity of the vascular strands which supply the rootlets. Similarly, vestiges of "aggregate" rays occur in the first formed portions of vigorous shoots and roots of *Alnus mollis* Fernald, *Alnus acuminata* H.B.K., and *Ostrya virginiana* (Mill.) Koch, species which do not possess "aggregate" or "compound" rays in the normal mature wood.

The structure of vigorous mature shoots of *Quercus velutina* and *Q. rubra* is also significant. As is well known, the primary vascular bundles of the oak are not grouped about a more or less cylindrical pith (except in the peduncle and epicotyledonary region), but about one that is deeply fluted (figs. 9 and 10). In cross-section the young twigs possess, therefore, a cambium layer that is composed of ten alternating convex and concave arcs. Thus five large wedge-shaped segments of secondary xylem are formed, which include between them five narrow depressed segments with more nearly parallel sides. This condition may persist in some cases for a number of years, but usually is replaced sooner or later by a stem of cylindrical outline. Vigorous shoots of the red and

black oak (fig. 19) resemble the normal stem of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these so-called primary rays increase in breadth as do those of the vigorous seedling stem (fig. 3), peduncle (fig. 8), and beech (fig. 1). The multiseriate rays which occur in the first annual ring of the narrow depressed segments gradually decrease in width during the next two years' growth and become uniseriate.

The structure and development of rays in the first annual ring of mature shoots are subject, as in the seedling stem, the root, and the peduncle, to marked variations under different physiological conditions. Thus wide rays show a strong tendency to become more numerous and parenchymatous in vigorous, well nourished shoots than in feeble, stunted, or suppressed twigs.

TRAUMATIC REGIONS

JACKSON called attention to numerous cases of reversion to supposedly ancestral types of structure under abnormal growth conditions or as a result of traumatism. JEFFREY, working largely with the internal structure of the gymnosperms, has emphasized the importance of traumatic reactions in the study of phylogeny. His contribution upon recapitulations in those regions of the plant which are assumed to be conservative, such as the root and seedling, is particularly significant, since injuries in these regions are said to recall ancestral characters when reversions cannot be induced traumatically in the mature stem.

The wound reactions of the Fagales are accordingly of interest in a consideration of the "aggregate" ray hypothesis. It has been found by the writers that the stimulating and irritating effect of certain types of injuries (whether mechanical or pathological) often accelerates the development of wide rays. The results of very severe injuries which have a marked distorting effect upon the tissues subsequently formed by the cambium are in some cases very different from these. Such injuries retard the development of large rays, just as feeble or stunted growth has been shown to retard the development of wide rays in seedlings and roots.

The stimulus of certain injuries may produce "aggregate" or multiseriate rays in plants or portions of plants which normally do not possess these structures. For example, when infected with the chestnut bark disease, *Endothia parasitica* Murrill, the chestnut may form large, completely parenchymatous sheets of ray tissue (fig. 16), just as "aggregate" or false rays may be recalled in the stems and roots of Betulaceae which normally possess only uniseriate rays (fig. 12). Wide multiseriate rays may also be induced in certain of the Betulaceae by traumatic stimuli. Especially significant are the effects of injuries in seedlings, roots, and the first formed portions of the mature shoots. Injured seedlings of *Quercus velutina* show an abrupt transition from congeries of uniseriate rays to wide sheets of homogeneous ray parenchyma. Furthermore, a seedling stem or root of *Quercus alba*, which possesses only uniseriate rays, will, when injured, form wide multiseriate rays (fig. 21). These rays often develop without indication of the putative stages of "compounding" (fig. 6). Similar phenomena occur in the first formed portion of mature shoots, in those radii of the stem which do not normally possess wide rays (fig. 10).

Discussion of evidence from conservative regions

In applying HAECKEL'S doctrine of recapitulation, the fact that plants develop by the activity of growing points or meristems rather than by interstitial growth has not always received sufficient consideration. Among higher animals the embryonic and very plastic stages of development are replaced by more highly organized and stereotyped conditions during early stages of ontogeny. In plants, however, the undifferentiated meristematic tissues retain much of their primitive plasticity throughout the life of the individual. This is shown by the fact that the growing points or meristems of mature plants are potentially able to reproduce the whole organism. Owing to this fact, that embryonic types of tissue are active throughout the life history of plants, phenomena of recapitulation need not be confined necessarily to the so-called seedling plant, and may be expected to be more varied than in the higher animals. Thus, there appears to be no fundamental a priori objection to the supposed natural conservatism of the first

annual ring, root, node, reproductive axis, or any other particular region. However, the meristematic tissues of the developing plant are in all probability more subject to modifying environmental influences than are the embryos of the higher animals. It is therefore not at all surprising that in many cases the normal conservatism of the embryonic tissues in any region should be more or less neutralized by local physiological changes in the same way that reversions to a more primitive type of structure may be recalled by abnormal stimuli or by traumatism. Nor is it necessary to suppose that all regions of the plant will be subject simultaneously to similar modifying influences. In any given individual or group of individuals, palingenetic characters may occur in one or more regions when they have been lost or replaced by cenogenetic structures in others. It may be seen, therefore, that very misleading conclusions will undoubtedly be drawn by assuming that a given character which appears in a certain conservative region of the plant is primitive, unless reliable corroborative evidence exists. In determining the possible antiquity of a given character it is essential that its structure, development, and behavior under different environmental and physiological conditions should be studied and compared throughout each representative of a wide range of living and, if possible, of fossil forms.

The results of such investigations are in general most conclusive when concerned with categories of characters which have been termed "degradational" or "regressive," that is, characters which are being reduced or lost. JACKSON ('99), in his study of the leaves of a number of gymnosperms and angiosperms, has contributed much toward the elucidation of the behavior of these characters. He has shown that in plants which are losing foliar characters by reduction or simplification the ancestral structures are recalled on vigorous, well nourished stems, or in tissue subject to stimulating types of injury. On the other hand, stunted, feeble, senile conditions tend to hasten the process of reduction, just as on stunted or sickly mature twigs or very old specimens, of a species which has not suffered reduction; the leaves may undergo an incomplete development and revert to the seedling type through a failure in their individual ontogeny to develop full specific char-

acters. The suppression of characters may progress in two ways. In most cases, the young plant, although more conservative in acquiring new foliar characters, is more retentive of these characters, once they become firmly fixed, than are most regions of the mature stem. On the other hand, marked changes in the environment or physiological activity of the young plant may more or less neutralize the effects of its natural conservatism. Under such conditions the seedling may develop cenogenetic characters or lose structures which are retained in mature portions of the plant. Thus JACKSON and COPE have shown that animals and plants may lose ancestral characters by "retardation of development. That is, features may appear at later and later stages in development until they finally disappear."

Internal structures appear in general to behave in regression and progression much as do external foliar characters. That vigorous or stimulated types of growth tend to recall characters which have been reduced has been illustrated, for example, by the recurrence in such types of tissue of marginal tracheids in the Cupresseae, of resin canals in the Taxodieae, and of wood parenchyma in the later Araucarieae. It also seems to be true that the influence of vigor and stimulating injuries in recalling reduced characters are most effective in regions which are supposed to be conservative, such as the first annual ring, root, node, and reproductive axis.

In the Fagales there is apparently a very complete series of species in which the successive stages of the reduction of wide multiseriate rays can be traced in detail. This process of reduction has taken place in most species by "retardation of development," accompanied by a greater or less degree of disintegration of the wide sheets of ray parenchyma. Unusually stimulating types of growth or traumatism recall the wide rays in regions from which they have disappeared or cause the cambium to form less complete stages of the disintegration process. These stimuli are often most effective in those regions of the plant which are supposed to be conservative, such as the first annual ring of roots and shoots, the seedling stem, and node. In the process of reduction the tissues near the entering traces of the leaves and rootlets and the peduncle

are particularly retentive of primitive, unreduced characters. Stunted, suppressed, or poorly nourished cambiums hasten the reduction of wide rays by an incomplete development of specific characters. The sensitiveness of wide rays to changes in the environment or physiological activity of the plant might be anticipated when we consider the function of these sheets of parenchyma as storage organs. It is not surprising, therefore, that the effects of conservatism should have been neutralized in certain regions of the plant.

A brief description of the comparative anatomy of species which occur at various levels in this "regression" series and their behavior under different physiological conditions follows:

Fagus grandifolia.—This plant illustrates diagrammatically the structure of a species in which the multiseriate rays have suffered little or no reduction. The stem (fig. 1) possesses a ring of primary fibrovascular bundles which are separated by well developed gaps. Those arcs of the cambium which bridge these gaps, the so-called interfascicular cambiums, form ray parenchyma exclusively. As a result of their activity, multiseriate rays are formed which vary in height and width as do the gaps in the vascular cylinder. In subsequent secondary growth these "primary medullary rays," which are 2–5 cells wide, increase gradually in width and may eventually attain a breadth of approximately 15–25 cells. Next the pith these rays are in the form of long vertical lines of parenchymatous tissue. As the stem develops, these tall rays or lines of superimposed high rays are dissected into shallower rays, which are gradually deflected from their original vertical axes. The so-called fascicular cambiums form at first tracheary tissue and uniseriate rays. The latter are also high in tangential section and form long lines which are dissected in subsequent development into shorter rays. Certain of these later increase in width and may in time become as wide as the rays of the so-called interfascicular segments. With the increasing circumference of the stem, new rays are formed continually by the cambium to maintain the proper proportion of ray tissue in each radius. These shorter "secondary" medullary rays which do not extend to the pith are uniseriate at first, but may increase in width during subsequent development. In any

annual layer of growth, therefore, there are rays one to many cells wide. In the first annual ring the widest rays occur in the vicinity of the nodes, on each side of traces which are about to enter the leaves.

The structure and development of rays in the ontogeny of secondary tissues in the seedling are fundamentally the same as in the mature stem. The root (fig. 2), which is commonly pentarch, possesses in cross-section five large rays that radiate from the five clusters of protoxylem. These rays are high and connect the traces of the rootlets. Although narrow when first formed, they widen rapidly and at the same time are dissected into shallower sheets of parenchymatous tissue. The other radii of the root possess at first only uniseriate rays, certain of which later increase in width as do some of the linear rays of the stem. Conditions such as have just been described occur in shoots and roots of normal development. The structure of wide rays is often different in suppressed, stunted, or feeble growth. Under these circumstances the first rays formed by the cambium are linear except in the vicinity of the traces which enter the leaves and rootlets, where multiseriate rays are persistent. In the stem the reduction of wide rays consists principally in the gradual narrowing of the sheets of parenchyma at their inner ends. In the root and the hypocotyledonary region, however, where the rays are often of considerable width, the reduction may be accompanied by slight indications of disintegration or dissection. If a shoot or root of this type receives a stimulating injury or develops suddenly a more normal type of vigor, an abrupt transition from uniseriate to wide multiseriate rays takes place, so that arcs of the cambium that have been forming linear rays and tracheary elements suddenly form only ray parenchyma (fig. 5). The phloem portion of the wide multiseriate rays, particularly in the stem, is characterized by a somewhat modified form of ray tissue. The cells of the rays become thick-walled and sclerenchymatous. At the same time the formation of ray cells upon the xylem side of the cambium is retarded, so that wedges of ray sclerenchyma project from the phloem into the xylem cylinder.

Quercus rubra.—The peduncle and the well nourished seedling stem or vigorous yearling twig of red oak resemble the normal

twig of *Fagus grandifolia*, since the gaps which separate the numerous distinct clusters of protoxylem subtend an equal number of multiseriate rays. There is this difference, however, that in subsequent growth of the twigs not all of these rays increase in breadth, as do those of the vigorous seedling stem and peduncle. The multiseriate rays which occur in the first annual layer of growth of the narrow depressed segments (fig. 9) gradually decrease in width during the next two years' growth and become uniseriate. That these rays are vestiges of wide rays which have been reduced by the arrested development of the depressed segments is indicated by the fact that when the cambium loses its specialized lobed form and releases these segments, one or more of the rays may eventually increase in width from uniseriate to multiseriate. In addition, it is interesting to note that a stimulating type of injury causes these reduced rays to resume their multiseriate form.

The "secondary" multiseriate rays which are formed as the stem increases in circumference are wider and arise more abruptly than do those of the beech. These rays may be formed by the rapid widening of a simple uniseriate ray or may show indications of incipient retardation of development and be disintegrated slightly at their inner ends.

The reduction of multiseriate rays is conspicuous in feeble, poorly nourished seedlings or in stunted or suppressed twigs (figs. 4 and 10). Under such conditions of reduced vitality the first formed portions of the seedling plant may possess only uniseriate rays, although the outlines of the suppressed wide rays are clearly marked; for each gap between the primary vascular bundles subtends an aggregation of uniseriate rays or a band of tissue that is entirely devoid of vessels. These "trails," or so-called "false" rays, radiate outward and in turn subtend the multiseriate rays which are eventually formed during subsequent growth. The retarded development of "secondary" multiseriate rays is likewise marked by a trail of aggregated small rays and tissue devoid of tracheae. If the cambium of a feeble seedling receives a stimulating injury or suddenly increases in vigor, multiseriate rays are recalled at once and appear abruptly in those radii from which they have been lost.

The retardation of the development of wide rays in stunted or suppressed twigs is also marked by short trails of disintegrated ray parenchyma and tissue devoid of vessels. This process of reduction is least conspicuous, however, in the vicinity of the entering traces and in the five pairs of wide rays which separate the depressed segments from the wider wedge-shaped ones. It is not uncommon, therefore, to find in the cross-section of a young twig that during their first activity the so-called interfascicular arcs of the cambium have formed multiseriate rays in certain radii of the stem and disintegrated sheets of ray parenchyma or tissue devoid of vessels in others. As in the case of poorly nourished seedlings, stimulating types of injuries or increased vigor recall the multiseriate rays in those radii of the stem in which they have suffered suppression or disintegration.

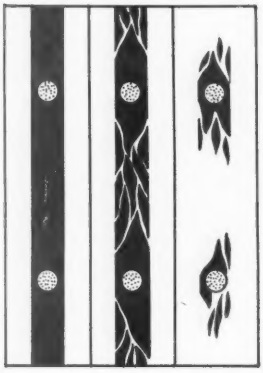


FIG. 1.—*A*, tangential section of a young root of *Fagus*, showing the vascular elements of two rootlets connected by a multiseriate ray; *B*, *Quercus* (subgenus *Erythrobalanus*), showing incipient stages of the disintegration of a wide multiseriate ray; *C*, *Quercus* (subgenus *Lepidobalanus*), showing vestiges of a multiseriate ray persisting about the vascular elements of the rootlets.

In vigorous young roots, wide multiseriate rays radiate outward from the clusters of protoxylem. These rays, as in *Fagus grandifolia*, form long vertical sheets of parenchyma which connect the traces of the outgoing rootlets (text fig. 1). Although these "primary" rays do not show well marked signs of incipient reduction, the broad alternating "secondary" multiseriate rays are in most cases considerably disintegrated at their inner ends. In less vigorous roots the primary multiseriate rays may also show evidences of reduction. However, the disintegration of these rays is most strongly shown usually at some distance from the strands of vascular tissue which supply the rootlets. Stimulating injuries or increased vitality recall the wide rays in regions of the root where their development has been retarded.

Quercus alba.—The reduction of wide multiseriate rays has progressed much farther in this oak of the subgenus *Lepidobalanus* than it has in most species of the subgenus *Erythrobalanus*, for even in vigorous, well nourished shoots and roots vestiges of wide rays persist, in the first formed secondary xylem, only in the vicinity of traces of the leaves and rootlets (fig. 6). The withdrawal of multiseriate rays from the mature shoots is accompanied by slight evidences of disintegration, but in the cotyledonary region and particularly in the root the very wide multiseriate rays are subtended by longer trails of disintegrating ray parenchyma and tissue devoid of vessels. With decreasing vigor, the multiseriate

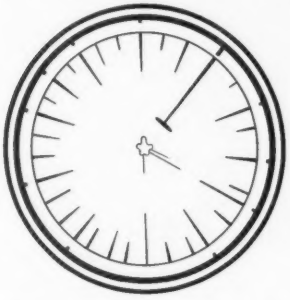


FIG 2.—Transverse section of a suppressed, forty-year-old branch of a mature specimen of *Quercus alba*, showing the retarded development of wide rays.

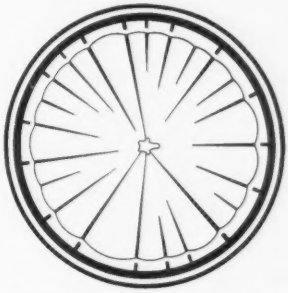


FIG. 3.—Transverse section of a vigorous, eleven-year-old shoot taken from the same tree as the suppressed branch illustrated in fig. 2.

rays appear at progressively later stages in the development of the stem and root (text figs. 2 and 3), but may be recalled by stimulating injuries or improved growth conditions.

Quercus virginiana.—In this evergreen or live oak the reduction of multiseriate rays has been carried farther than in either of the preceding species. The wide rays are commonly absent in young stems, but may be well developed in the vicinity of the vascular elements which pass out to the rootlets (fig. 17). When the wide rays appear during subsequent growth, they are much disintegrated and may persist in this dissected condition for many years, although in some cases they may finally become homogeneous ray parenchyma. This tendency for large multiseriate

rays to become disintegrated not merely at their inner ends but throughout their ontogenetic development is characteristic of many tropical or subtropical species of *Quercus*. Severe, stunting types of injuries hasten the disintegration of the sheets of ray tissue, whereas stimulating or irritating injuries cause reversions to wide multiseriate rays.

Castanea dentata.—The common sweet chestnut illustrates a case in which the reduction of multiseriate rays is nearly complete. Vestiges of wide, multiseriate rays occur, however, in the first formed tissue of very vigorous roots (figs. 11 and 20) and shoots in the vicinity of the traces which pass out to the leaves and rootlets. Multiseriate rays may also be recalled by stimulating types of injuries such as are produced by the irritating effects of infections of *Endothia parasitica* (fig. 16). It is interesting to note that not only is the oak type of ray recalled but also the oak type of fiber-tracheid and leaf (fig. 18).

Betulaceae.—In the Betulaceae the reduction and disintegration of wide rays is far advanced. Typical wide multiseriate rays occur, however, somewhat sporadically in the stems of *Alnus rhombifolia* Nutt. and *A. maritima*, or may be recalled by stimulating injuries or vigorous growth in regions which do not normally possess them. In most species the rays have become entirely disintegrated except in the peduncle, where narrow multiseriate rays may be persistent. As the process of reduction is continued, these sheets of dissected ray parenchyma are replaced gradually by aggregations of multiseriate rays, and finally by bands of tissue that are merely devoid of vessels. These trails or vestiges of former multiseriate rays, so-called false rays, are frequently persistent in the vicinity of the traces of the leaves (fig. 12) and rootlets, and may remain in these regions, particularly in the first annual ring of vigorous roots and shoots, after they have disappeared from the rest of the plant. This process of reduction is accelerated by stunted, suppressed growth and retarded by vigor. The less complete stages of reduction and disintegration are recalled by stimulating injuries and unusually vigorous growth.

We have seen above that the wide multiseriate rays of the Fagales are characterized by a peculiar sclerenchymatous modifica-

tion of their phloem extensions (figs. 1, 2, 7, etc.). It is significant, therefore, that these typical intruding wedges of sclerenchyma occur in the Betulaceae opposite each "false" ray of the xylem cylinder (fig. 12).

Casuarinaceae.—Successive stages of the reduction and disintegration of wide multiseriate rays, such as are found in the genus *Quercus*, occur in the shea-oaks or Casuarinas. There are several species in this family, however, in which the wide multiseriate rays are persistent in the first formed portions of the stem. In the subsequent development of these wide rays reduction and disintegration occur. These dissected sheets of smaller ray tissue become diffused through certain radii of the stem, and in this way wide multiseriate rays are replaced by narrower biseriate or triseriate ones. At the same time, certain of the uniseriate rays which occur between the wide rays widen until they become as broad as the narrow sheets of tissue which are dissected from the original wide ray. A somewhat similar phenomenon appears to have occurred in the genus *Betula*, in which narrow biseriate or triseriate rays have replaced the original wide multiseriate rays. As in the Fagales, wide multiseriate rays may be recalled in the Casuarinaceae by stimulating growth or injuries, and tend to be persistent in the peduncle and the vicinity of the traces of the leaves and rootlets.

Origin, distribution, and antiquity of multiseriate rays

Multiseriate rays of varying width are well developed in the majority of arborescent or shrubby dicotyledons and may be traced through the Tertiary to the Middle Cretaceous. These sheets of parenchyma characterize the great tropical families of woody dicotyledons, as well as those which live in a more temperate habitat. Very wide multiseriate rays occur in presumably specialized types, such as lianas, mangroves, desert plants, semi-herbaceous shrubs, etc., which are adapted to peculiar environments. The investigation of the structure and development of rays in the various families of the dicotyledons reveals much evidence that the multiseriate rays originated by the gradual widening of primitive uniseriate rays. Detailed evidence in favor of this view will be given by the writers in a subsequent paper.

Summary and conclusions

The "aggregate" ray hypothesis developed by JEFFREY and amplified by a number of students working under his direction has an important bearing upon the phylogeny of the angiosperms, since it indicates that certain of the Amentiferae are in all probability the most primitive living representatives of the phylum. There appear to be serious objections to this hypothesis, however.

OBJECTIONS TO THE "AGGREGATE" RAY HYPOTHESIS

1. The phenomenon of chalazogamy, which was considered at first of great phylogenetic value, cannot, in view of later investigations, be considered a reliable criterion for determining the phylogenetic position of plants.

2. The occurrence of so-called "aggregate" rays in the Tertiary does not appear to be significant, since "multiseriate" rays, which are considered to be a comparatively recent adaptation to the advent of a severe winter season and the consequent acquirement of the deciduous habit, are found in middle and upper cretaceous dicotyledons.

3. If "aggregate" and "compound" rays originated for the purpose of storing the assimilates descending from the persistent leaves of angiosperms in the warmer times of the Mesozoic and were later replaced by "multiseriate" rays as an adaptation to a period of refrigeration, we should hardly expect to find multiseriate rays well developed in families which have lived in tropical environments since ancient times.

4. The "aggregate" ray, which is comparatively infrequent, characterizes the obviously reduced xerophytic Casuarinaceae, and the temperate families Betulaceae, Fagaceae, and Ericaceae.

5. The "aggregate" ray hypothesis does not account for the development of "secondary" multiseriate rays nor for the origin of wide rays in the root.

6. The seedling evidence which has been advanced in favor of the origin of wide rays from congeries of uniseriate rays is invalidated by the occurrence of wide multiseriate rays in seedlings of oaks, and also in such supposedly conservative regions in this genus as the node, root, reproductive axis, and first annual ring.

"AGGREGATE" RAYS STAGES IN THE REDUCTION AND DISINTEGRATION OF WIDE MULTISERIATE RAYS

In the Fagales and Casuarinaceae there is a very complete series of form in which the progressive reduction and disintegration of wide multiseriate rays can be traced in detail. During this process of reduction the wide rays appear usually at later and later stages in ontogeny, until they finally disappear. The so-called "aggregate" rays are stages in the disintegration of wide multiseriate rays. Stimulating types of growth and injury recall the wide rays in regions where they have been lost, and are frequently most effective in those regions which are supposed to be conservative, such as the first annual ring, root, node, and seedling. Stunted, suppressed, poorly nourished types of growth, and severe distorting injuries hasten the reduction and disintegration of the wide multiseriate rays. In this process of reduction vestiges of the wide rays tend to be more persistent in the peduncle, root, and nodal regions.

THE MULTISERIATE RAY A WIDENED UNISERIATE RAY

The multiseriate ray does not appear to be of recent origin, since it is well developed in most tropical and temperate families and extends through the Tertiary at least to the Middle Cretaceous. This type of ray structure originated in all probability by the gradual increase in width of the primitive uniseriate ray.

PHYLOGENY OF THE AMENTIFERAE

One character, of course, cannot be considered conclusive evidence for assuming that a plant or group of plants is "regressive" or reduced, since all characters will not be similarly affected by changes in the environment or physiological activity, but the reduction of wide rays in the Fagales indicates that this order, as well as the Casuarinaceae, has been subjected to a strong modifying influence. This fact, taken together with the occurrence of syncarpy, epigyny, abortive ovules, and vestiges of bisexual flowers and floral envelopes, emphasizes the importance of the frequently repeated suggestion that the Amentiferae, instead of being the most primitive of angiosperms, are a group of specialized families

which have reached their present more or less simple structure through reduction from earlier and usually more complicated forms.

BUSSEY INSTITUTION
HARVARD UNIVERSITY

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EXPLANATION OF PLATES III–V

FIG. 1.—Transverse section of a seedling stem of *Fagus*, illustrating the structure, development, and distribution of multiseriate rays which have not suffered reduction.

FIG. 2.—The same; young root.

FIG. 3.—Transverse section of a vigorous young seedling stem of *Quercus rubra*, showing multiseriate rays which radiate from each wide gap in the primary elements.

FIG. 4.—The same; less vigorous seedling stem, showing the disintegration and reduction of wide rays and their recurrence in tissue which has been formed under the stimulating effects of an injury.

FIG. 5.—Transverse section of a suppressed seedling of *Fagus*, showing the arrested development of wide multiseriate rays in the first formed portion of the hypocotyledonary stem and their sudden recurrence after a stimulating type of injury.

FIG. 6.—Transverse section of a young root of *Quercus* (subgenus *Lepidobalanus*), showing the reduction of multiseriate rays; "trails" of aggregated uniseriate rays mark the former position of the wide rays; in one radius vestiges of a multiseriate ray have persisted in the vicinity of the outgoing vascular elements of a rootlet; in another portion of the root a stimulating type of injury has recalled wide homogeneous sheets of ray parenchyma.

FIG. 7.—Transverse section of the seedling stem of *Casuarina suberosa*, showing the disintegration and reduction of wide rays.

FIG. 8.—Transverse section of a peduncle of the same species, showing well developed multiseriate rays.

FIG 9.—Transverse section of a vigorous young shoot of *Quercus* (subgenus *Erythrobalanus*), showing five depressed segments and multiseriate rays.

FIG. 10.—Transverse section of a stunted, slow growing branch of *Quercus* (subgenus *Erythrobalanus*), showing the reduction of multiseriate rays, their persistence on either side of the depressed segments, and their recurrence in tissue stimulated by injuries.

FIG. 11.—Transverse section of a very vigorous young root of *Castanea dentata*, showing the persistence of vestiges of wide rays in the vicinity of the vascular elements which supply the rootlets.

FIG. 12.—Transverse section of a shoot of *Alnus*, showing the persistence of "trails" of uniseriate rays about the lateral leaf-traces and their recurrence in traumatic tissue.

FIG. 13.—Transverse section of a portion of a vigorous seedling stem of *Quercus rubra;* two multiseriate rays radiate from the gaps between three clusters of primary elements; ×45.

FIG. 14.—Transverse section of a portion of a less vigorous seedling stem of *Quercus rubra*, showing the reduction and disintegration of two multiseriate rays; ×45.

FIG. 15.—Transverse section of part of a two-year-old peduncle of *Quercus coccinea*, showing multiseriate rays; ×80.

FIG. 16.—Transverse section of traumatic tissue of *Castanea dentata*, showing oaklike multiseriate rays and fibers recalled by the stimulating effects of *Endothia parasitica;* ×130.

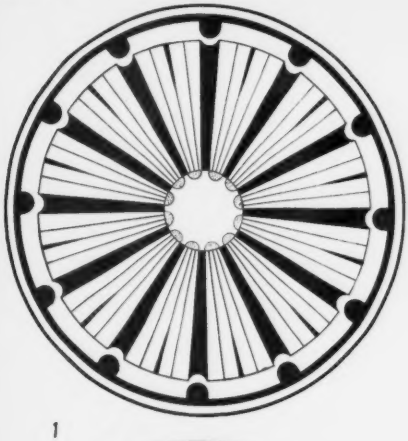
FIG. 17.—Transverse section of a portion of the hypocotyledonary stem of *Quercus virginiana*, showing wide multiseriate ray subtended by protoxylem; ×20.

FIG. 18.—Reversionary leaf of *Castanea dentata*, showing oaklike characters recalled by the stimulating effects of *Endothia parasitica;* ×½.

FIG. 19.—Transverse section of the first formed portion of a depressed segment of a vigorous shoot of *Quercus velutina;* multiseriate rays radiate from each gap in the primary vascular cylinder; ×45.

FIG. 20.—Transverse section of the first formed portion of a very vigorous root of *Castanea dentata*, showing vestiges of multiseriate rays; ×15.

FIG. 21.—Transverse section of the primary root of *Quercus alba*, showing the recurrence of multiseriate rays under the stimulating effects of an injury; ×5.



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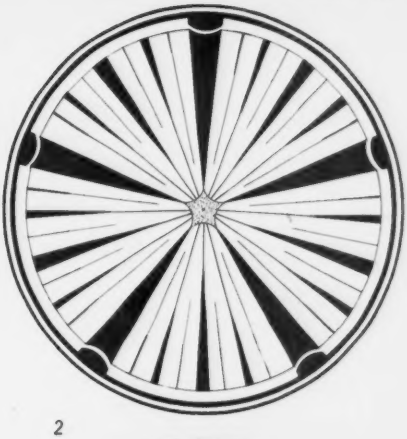

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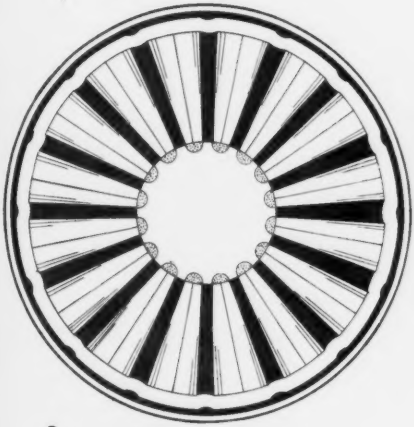

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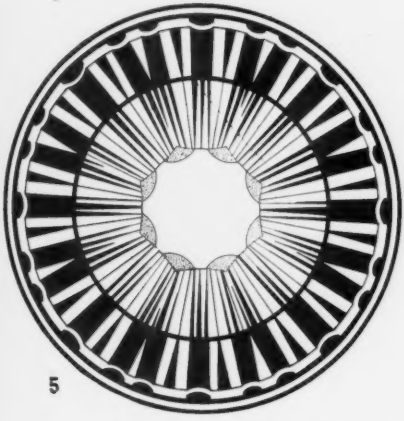

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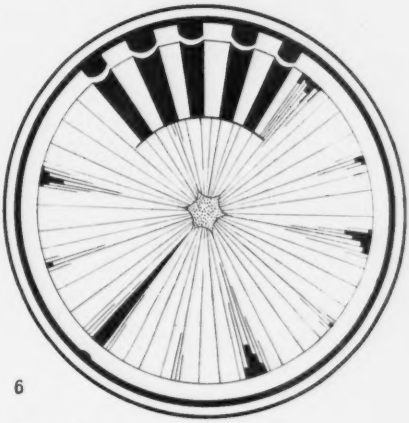

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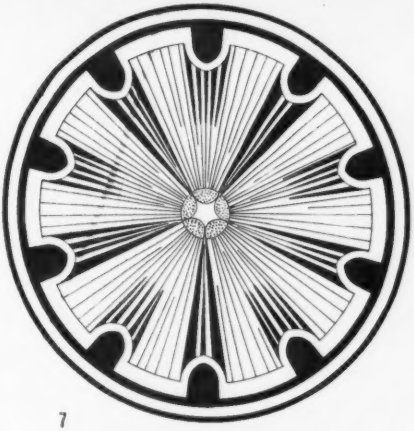
BAILEY and SINNOTT on PHYLOGENY OF ANGIOSPERMS



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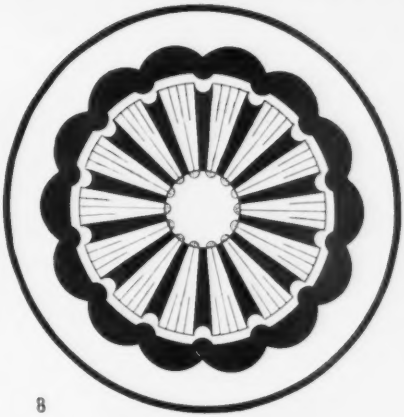

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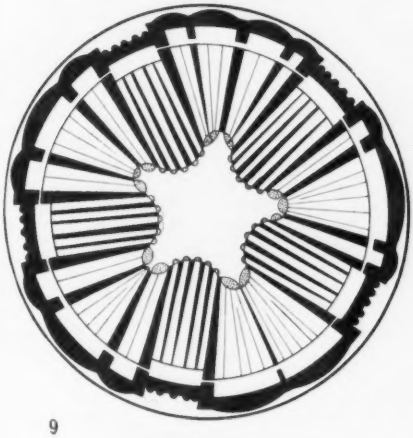

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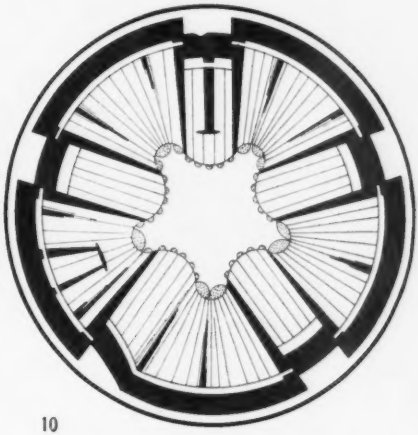

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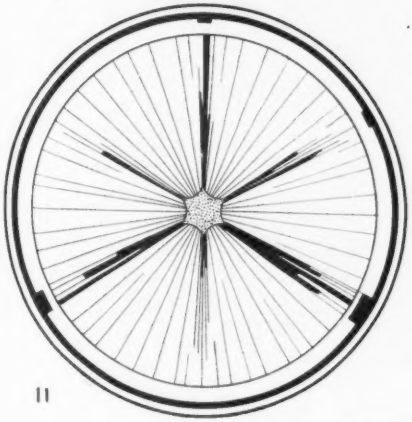

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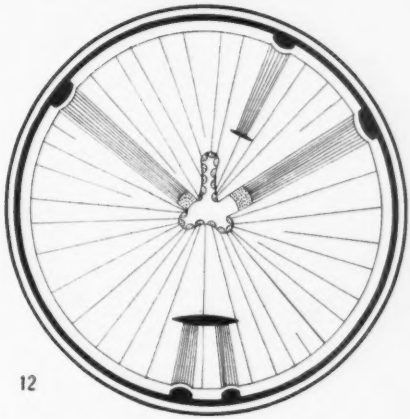

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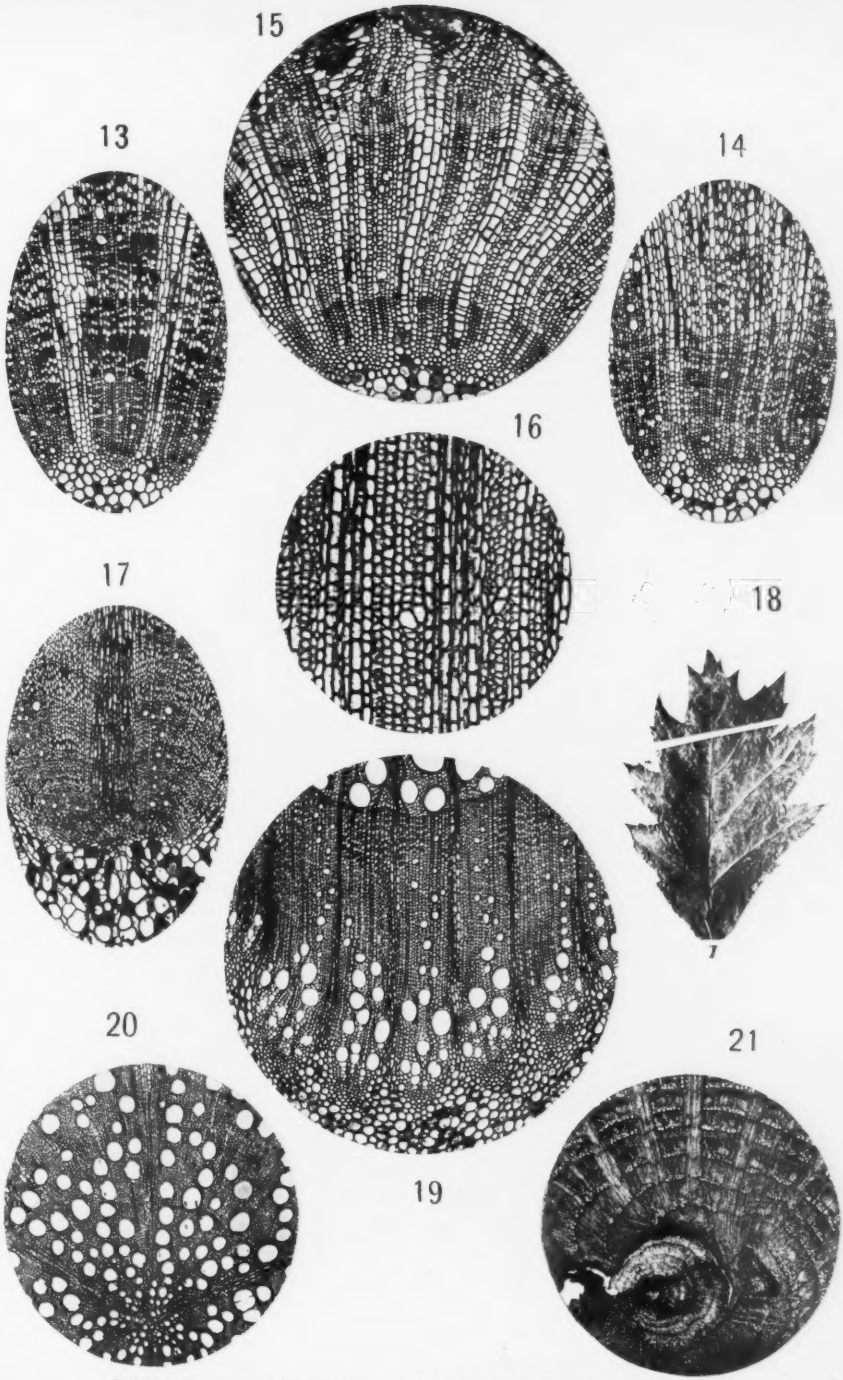


BAILEY and SINNOTT on PHYLOGENY OF ANGIOSPERMS

THE ANATOMY OF SIX EPIPHYTIC SPECIES OF LYCOPODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 189

J. BEN HILL

(WITH TWENTY-EIGHT FIGURES)

In this investigation, six epiphytic species of *Lycopodium* were studied. Two New Zealand species, *L. Billardieri* Spring. and *L. varium* R. Br., with two South African species, *L. verticillatum* G.f. and *L. Holstii* Hieron., were furnished by Dr. CHARLES J. CHAMBERLAIN; and two forms from Samoa, *L. Phlegmaria* Linn. and *L. carinatum* Desv., were collected by Dr. W. J. G. LAND. The two species from New Zealand were identified by Dr. JESSE M. GREENMAN of the Field Museum, Chicago, and the remainder were identified by Dr. G. HIERONYMUS of Berlin. There was some doubt concerning the identity of the two forms from Samoa, since they do not correspond exactly to the descriptions of their respective species. Dr. HIERONYMUS suggests that each represents a new variety or subspecies. The species studied are described as growing epiphytic upon trees, with the short, vegetative branches more or less erect, and the long, slender, dichotomously branched strobili pendulous (fig. 1). Most of these species are rather rare, but *L. Phlegmaria* and *L. Billardieri* are mentioned in the recent literature dealing with the morphology of the group. Since these forms are not very familiar to residents of the northern hemisphere, a short general description may serve to make this account more intelligible.

L. Holstii is a very coarse plant, with short thick stems covered with large stiff leaves. The stem is 4–6 mm. in diameter, with a small stele 0.35 mm. in diameter. The leaves are about 2.5 cm. long and sharply pointed. Type material, furnished by Dr. G. HIERONYMUS, shows sporophylls with little or no modification from the vegetative leaves. They are not grouped in a definite strobilus, but are simply aggregated near the apex, much as in *L. lucidulum*.

FIG. 1.—*L. Phlegmaria:* epiphytic upon cocoanut tree; photograph of the plant in the field showing the habit of the species, by LAND.

L. verticillatum is much more delicate, with a slender stem covered with long, slender leaves. The sporophylls are arranged in definite strobili, which are regularly dichotomously branched and attain a length of 20–40 cm. The sporophylls show a slight modification from the foliage leaves, being smaller and more sharply pointed. Both leaves and sporophylls show spiral phyllotaxy.

L. Billardieri and *L. varium* resemble each other in their general appearance. Both bear long, dichotomously branched strobili with cyclic sporophylls arranged in alternating pairs, so that the outline in transverse section is square. In both species the sporophylls differ from the foliage leaves, being short and bluntly pointed. The chief gross difference in the two species is that *L. varium* is slightly coarser and the square shape of the transverse section of the strobili seems to be more definitely fixed than that of *L. Billardieri*, which produces some strobili circular in transverse section.

L. Phlegmaria is well known and needs little description. It is one of the most conspicuous examples of dimorphic leaves, the sporophylls being very small and delicate, almost membranous, while the vegetative leaves are broad and short. The strobili are very definite because of the extreme modification of the sporophylls and are circular in transverse section. Both vegetative leaves and sporophylls are sometimes cyclic in arrangement.

L. carinatum probably represents the highest specialization of any of the species studied. There is definite dimorphism of the leaves, which show the cyclic arrangement to the extent of giving even the young shoots the quadrangular appearance so characteristic of the strobili of some epiphytic lycopodiums. The strobili are also square in transverse section and dichotomously branched. The anatomical study also justifies the statement that this species represents the highest specialization of the species studied.

The material from New Zealand consisted entirely of mature stems and strobili, with no vegetative shoots. Roots were present in the material of *L. Billardieri*. The material of *L. verticillatum* consisted of several complete mature plants with both vegetative shoots and strobili, while that of *L. Holstii* was entirely vegetative.

The two species from Samoa were complete. No prothallia nor young sporophytes were present in any of the material. An investigation of the anatomical structures of the plants offered the most interesting feature of study, and this investigation was undertaken with reference to the development of the stele and its bearing upon phylogeny. The material was studied from paraffin serial sections cut 10–15 μ in thickness and stained in safranin-anilin blue and in safranin-light green. Since the material of *L. carinatum* was complete, and of such a character as to show the structures especially well, this species was selected as a basis for description and comparison.

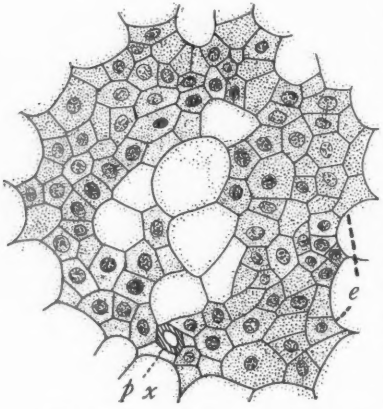


FIG. 2.—*L. carinatum:* transverse section of the stem near the apex, showing the organization of the young stele; *e*, inner wall of endodermal cells; *px*, protoxylem; large cells in center are unlignified potential metaxylem cells; ×500.

L. carinatum

In the apex of the strobilus of *L. carinatum* the outline of the transverse section of the young vascular cylinder is often almost square. Within the first millimeter of the stem, before any lignification of the protoxylem is recognizable, there is distinct differentiation of the tissues; not only is the cylinder organized as a region distinct from the cortex, but the elements of the tissues of the vascular system are differentiated. The large cells of the endodermis are discernible, inclosing a mass of smaller cells, part of which have abundant cytoplasm and conspicuous nuclei. This group of cells is to be differentiated into the vascular tissues.

At this stage of development there are two distinct systems of cells within the stele. The central region of the young cylinder is occupied by 5–10 large, thin-walled, unlignified cells with vacuolate cytoplasm, forming an irregular radiating group. These are to become lignified and form metaxylem. The angles of this radiating

mass of cells and the portions of the cylinder just within the endodermis are occupied by groups of smaller cells which have relatively very large nuclei and dense cytoplasm. These smaller cells are the parenchyma of the cylinder and will give rise to both the protoxylem and the phloem elements (fig. 2).

The cylinder of the vegetative apex is more nearly circular in outline than that of the strobilus. The two show similar differentiation and differ little excepting that the cylinder of the vegetative shoot has about twice the diameter of that of the strobilus, and the extent of the group of large cells is greater, with more numerous groups of small parenchyma cells.

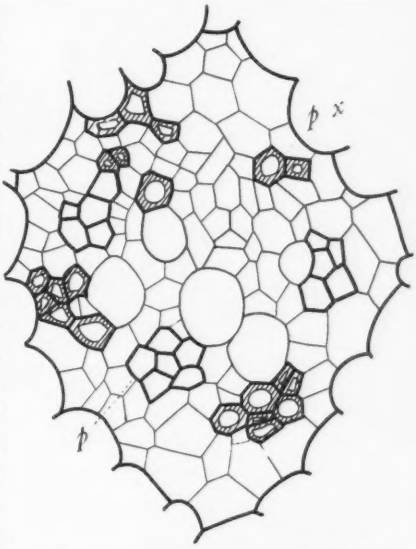
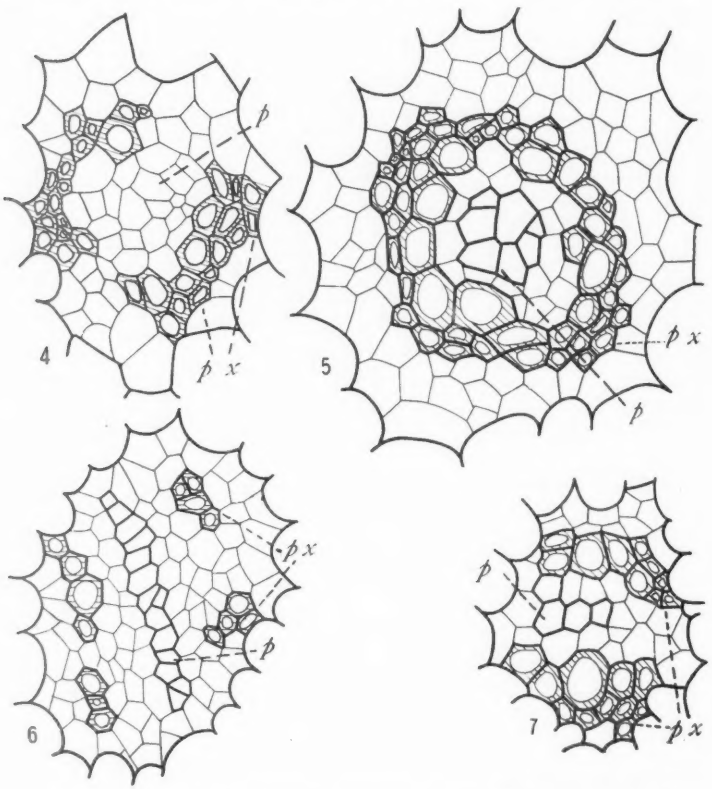


FIG. 3.—*L. carinatum:* transverse section of the strobilus axis, showing the radial arrangement; *px*, protoxylem; *p*, phloem; ×500.

In the further organization of the stele, the protoxylem is the first to be differentiated. The protoxylem points arise in irregular succession in the peripheral region of the cylinder by the lignification of some of the small cells. Generally there is only one cell lignified first, and usually this cell is situated in the second layer of cells from the endodermis. This is followed by the lignification of some of the adjacent smaller cells similarly situated. This leaves a pericycle, at first one layer of cells in thickness. There are 2–4 protoxylem points differentiated in the strobilus apex, and a large number, generally 6 or 8, in the vegetative apex. These points are located at the peripheral ends of the radiating strands of the central group of unlignified cells (fig. 3). This is the regular situation in the vegetative apex, but when there are only 2 protoxylem points in the strobilus apex, the relation of the protoxylem and the

unlignified cells may vary. Often the arrangement shows the protoxylem point on each side of the cylinder, with a band of unlignified cells arranged parallel to it and just inside, while the middle of the cylinder is occupied by a band of phloem extending



FIGS. 4–7.—Fig. 4, *L. carinatum:* transverse section of the strobilus apex, showing the development of the parallel-banded type; *px*, protoxylem; *p*, phloem; fig. 5, *L. carinatum:* transverse section of the stele in the strobilus axis, showing the amphivasal condition, phloem in the center inclosed by a ring of xylem; *px*, protoxylem; *p*, phloem; fig. 6, *L. Phlegmaria:* transverse section of strobilus, showing radial arrangement, with the phloem extending across the center forming a band; the same condition is also found in *L. carinatum; px*, protoxylem; *p*, phloem; fig. 7, *L. Phlegmaria:* showing the development of the parallel-banded stele; *px*, protoxylem; *p*, phloem; all ×500.

from the sides across the center (fig. 4). This gives the parallel-banded type of stele, that is, alternating parallel bands of xylem and phloem. In all of these situations there is a tendency for the protoxylem to grow around the circumference of the cylinder (figs. 8, 9), with very irregular behavior of the groups, consisting of fusions and splitting, resulting in crescent-shaped masses and even in masses completely encircling a central mass of the parenchyma and phloem, giving a type of stele resembling the amphivasal type found in monocotyledons (fig. 5).

The phloem as recognizable tissue is differentiated from the parenchyma at a somewhat later period than the protoxylem. In all of the protoxylem situations described above, the phloem arises from the small parenchyma cells located on the same circumference as the protoxylem, giving a true radial stele.

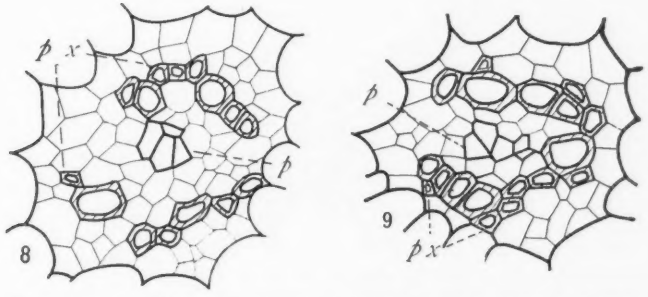
The study of the strobilus in transverse serial sections shows three types of stele: radial, parallel-banded, and amphivasal, the two latter conditions being derived from the first by modifications and specialization. These changes are not connected with branching. They are the result partly of the behavior of the protoxylem groups, but chiefly of the growth and development of the metaxylem. The young stele in the apex is organized at first with a distinct radial arrangement, the protoxylem points, 2 or 3 in number, alternating with phloem groups on the same circumference (fig. 3). Lower in the stem, the sections show the protoxylem extending around the periphery of the cylinder, with the developing metaxylem organized as two parallel bands, with the phloem groups at each end, extending inward and forming a central band of phloem (fig. 4). At a slightly lower level in the young strobilus, the amphivasal arrangement is found (fig. 5). This is a further modification of the parallel-banded arrangement. It is formed by the continued peripheral growth of the xylem until a complete ring is formed inclosing the phloem. This ring remains intact only a short distance in the stem. At a lower level it appears broken up into the parallel-banded types, and this condition still lower passes into the distinctly radial arrangement. Since the parallel-banded and radial arrangements are found both above and below the amphivasal, the latter passing into the parallel-banded, and that

into the radial, it is clear that these various conditions are all modifications of the radial arrangement (fig. 3). In most cases the amphivasal condition is not attained. This occurs where the xylem grows around only one end of the band of phloem, giving a crescent-shaped xylem (fig. 9). This arrangement may be either an intermediate condition between the parallel bands and the amphivasal situation, or it may represent the final development at that point and, breaking up, return to the parallel-banded type without the formation of the amphivasal. These modifications seem to be entirely confined to the strobilus cylinder. In the vegetative stems and in the vegetative part of the stem which bears the strobilus, there is no evidence of the modifications of the stele which are so characteristic of the strobilus. All vegetative parts are radial as to their stelar structure excepting where this condition is modified by branching.

At the base of the vegetative stems roots leave the stele, and pass downward through the cortex for some distance before finally passing out of the stem. These roots show a peculiar tendency to form a ring of xylem resembling the ring of xylem in the stem.

L. Phlegmaria and L. varium

Both these species greatly resemble *L. carinatum* in the tendency of the strobilus to develop the parallel-banded type of stele, by the peripheral growth of protoxylem and by the development of the metaxylem at the sides of the cylinder, leaving the central portion occupied by the phloem. This tendency to the peripheral growth of the xylem is especially marked in *L. varium*, where even in the mature stem it is sufficiently extensive to inclose one-third to one-half of the stele in certain portions for a considerable distance (fig. 15). *L. Phlegmaria* shows many crescent-shaped masses of xylem in the strobilus stele (figs. 8, 9), which nearly close, but it seldom if ever fully attains the amphivasal condition reached by *L. carinatum*. The parallel-banded type in *L. varium* is not always derived from the radial arrangement as it seems to be in *L. carinatum*. The apex shows distinctly two methods of organization of the stele. One is the radial as described for *L. carinatum* (figs. 10, 11). The other is the method in which the radial arrangement



FIGS. 8, 9.—*L. Phlegmaria:* transverse sections in the same series, showing the development of the crescent-shaped xylem mass from the parallel-banded type; the same method of development is found in *L. carinatum*, which carried farther gives the amphivasal condition; *px*, protoxylem; *p*, phloem; ×500.

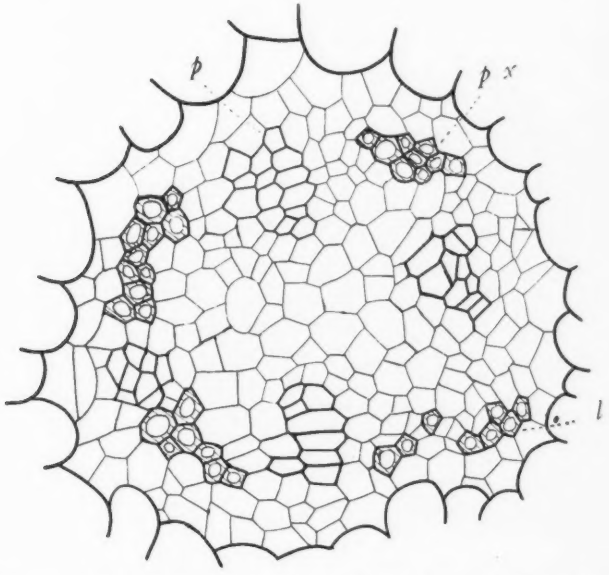


FIG. 10.—*L. varium:* transverse sections of the strobilus apex, showing the radial arrangement; *l*, leaf trace; *px*, protoxylem; *p*, phloem; ×500.

does not appear at first. There is one protoxylem point on either side with the phloem between, which develops directly into the parallel-banded types (figs. 12, 13). These parallel bands of xylem may develop into crescent-shaped xylem masses. The crescent-shaped xylem is a high development of the parallel-banded type of stele, formed, as in *L. carinatum*, by the growth of xylem around one end of the phloem (fig. 9). The mature stem and the vegetative

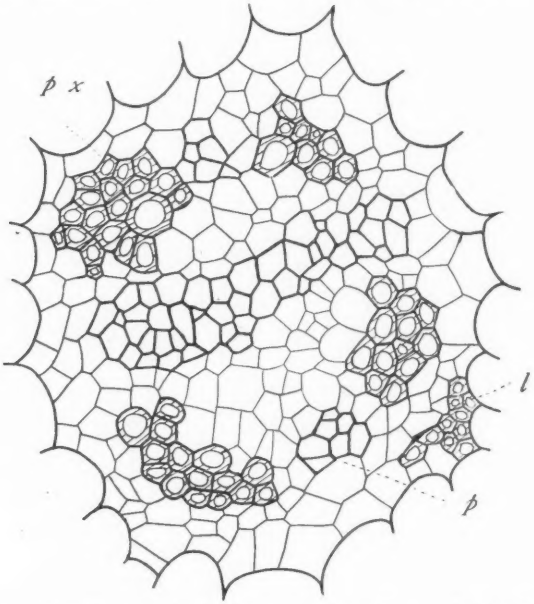
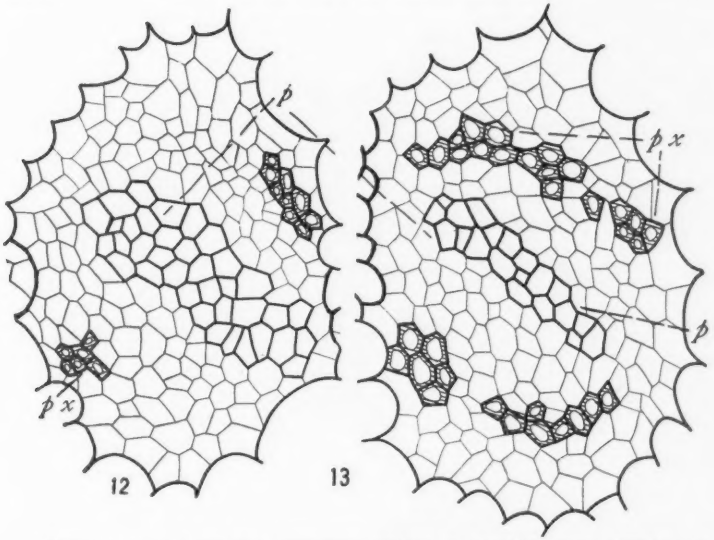


FIG. 11.—*L. varium:* section in the same series as fig. 10, showing the development of the parallel-banded type from the radial; *l*, leaf trace; *px*, protoxylem; *p*, phloem; ×500.

stem of *L. Phlegmaria* are characterized by the true radial arrangement (fig. 14). The material of *L. varium* was entirely strobilus-bearing, but the vegetative portions show the radial arrangement (fig. 15). The type of the stele in all cases in these species, as in *L. carinatum*, is determined by the growth of the metaxylem.

As an aid to a better understanding of these stems, clay models were made of the xylem portions of the steles by studying serial



FIGS. 12, 13.—*L. varium:* transverse sections of strobilus apex, showing the parallel-banded type of stele developing directly without passing through the radial arrangement; *px*, protoxylem; *p*, phloem; ×500.

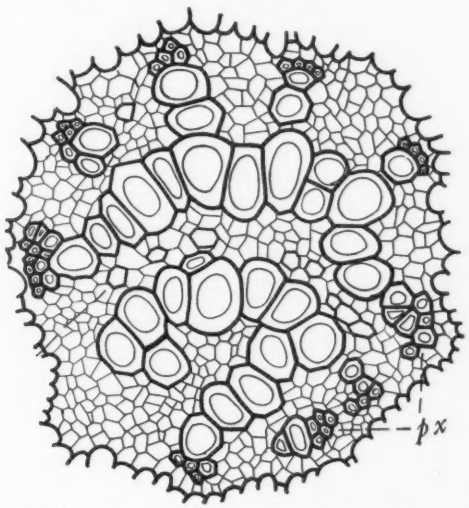


FIG. 14.—*L. Phlegmaria:* transverse section of mature vegetative stem; *px*, protoxylem; *p*, phloem; ×185.

sections and building up the corresponding structures in clay (figs. 16, 17). Vegetative portions were selected for reproduction and the method of study gave some interesting results. The model of the stele of *L. varium* was almost a complete cylinder, with occasional breaks in the peripheral shell of xylem (fig. 16). This structure is due to the growth of the xylem around the periphery. There were some indications that this growth is related

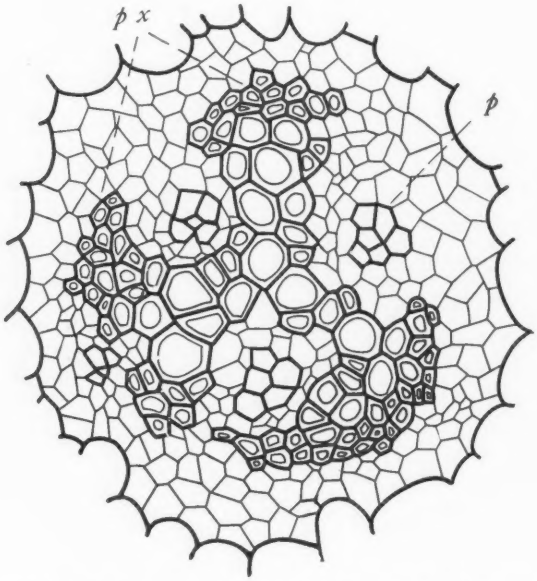


FIG. 15.—*L. varium:* transverse section of the strobilus-bearing branch, showing the radial arrangement; *px*, protoxylem; *p*, phloem; ×300.

to the passing out of the leaf traces, since often there would be a leaf trace at the point of meeting of two of the peripheral growths. There was too much irregularity in the matter of leaf traces to justify making any definite statements, since leaf traces pass off from the protoxylem points and from the peripheral growths also, with no apparent general relation to the growth of the xylem. The study of the clay models showed branching and fusions of the protoxylem points to be quite common. The relation of xylem

and phloem was evident in the model; the branching of the xylem was often followed by branching of the phloem groups and xylem fusions by phloem fusions. Frequently the peripheral

FIG. 16.—*L. varium:* photographs of the clay models of the stele; the base is started at the portion of the stem represented in fig. 15; the projections represent the leaf traces which pass out indiscriminately from the stele; *l*, leaf trace.

growth of the xylem cut off phloem on the outside of the xylem, and sometimes phloem seemed to arise outside when the xylem was indented.

FIG. 17.—*L. Phlegmaria:* photographs of the clay models of the stele; the ridges represent the projecting protoxylem groups which fuse and branch irregularly; leaf traces are represented by projections; *px*, protoxylem; *l*, leaf trace.

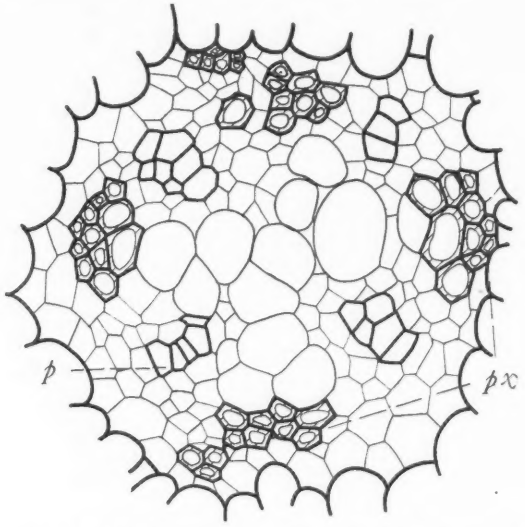


FIG. 18.—*L. Billardieri:* transverse section of the strobilus apex, showing the radial organization of the stele; protoxylem groups alternating with phloem; the center of the stele is occupied by the unlignified potential metaxylem cells; *px*, protoxylem; *p*, phloem; ×500.

L. Billardieri

The organization of the strobilus in this species is distinctly radial, and this condition was constant in all the material examined (fig. 18). The further development of the metaxylem also results in a very regular structure for the stem. This structure consists of several radiating bands of xylem with phloem groups between them. The xylem also has a great tendency to form an almost

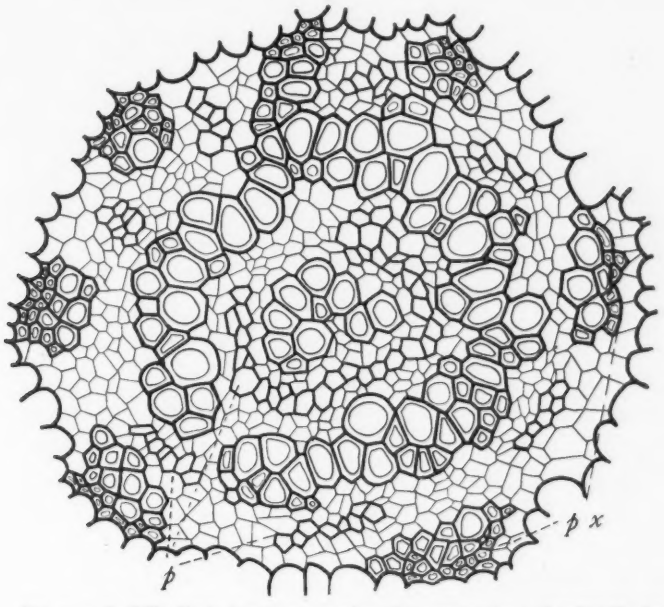


FIG. 19.—*L. Billardieri:* transverse section of a mature stem, showing the inner xylem ring; *px*, protoxylem; *p*, phloem; ×185.

complete ring inside the stele. The center of this ring may be occupied by a single isolated strand of either phloem or xylem. The development of the ring is dependent entirely upon the behavior of the metaxylem and not upon the peripheral growth as in *L. carinatum*, for it is not peripheral to the stele, but is located inside the periphery, forming an inner ring with radiating masses of xylem which extend to the circumference of the vascular cylinder (fig. 19).

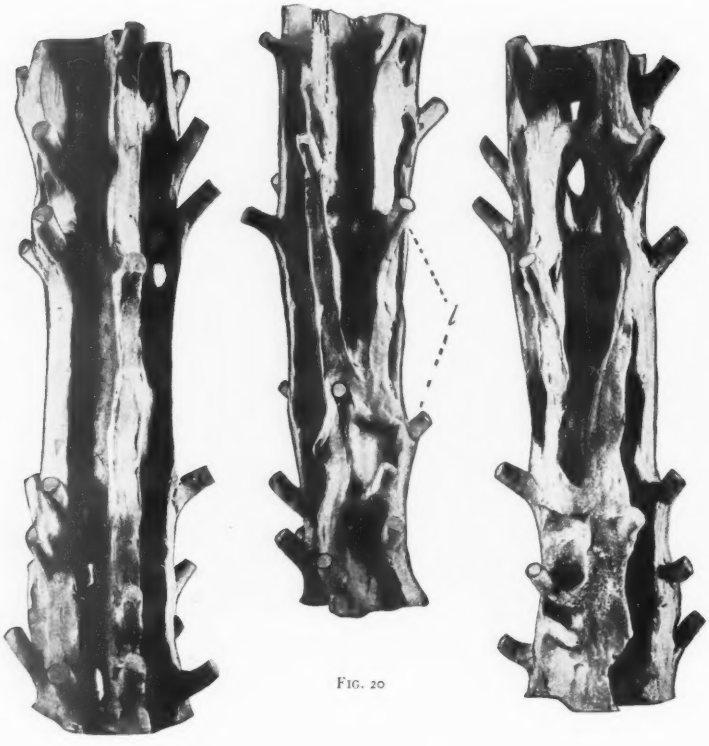


FIG. 20

FIG. 20.—*L. Billardieri:* photographs of the clay model, showing the irregular behavior of the protoxylem groups and their relation to the leaf traces; the protoxylem groups here show both fusions and splitting; *l*, leaf trace.

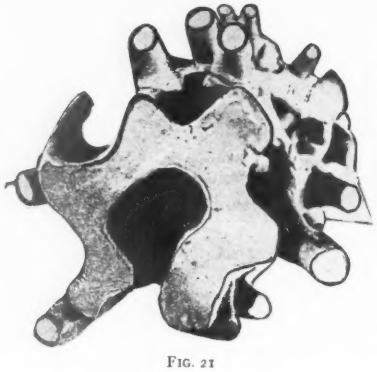


FIG. 21

FIG. 21.—*L. Billardieri:* photograph showing an end view of the model shown in fig. 20.

This is the usual condition of the vegetative portions of the stem and can be designated as a radial arrangement. A clay model of the xylem portions of the stele was made, and it shows something of the xylem behavior in the stem (figs. 20, 21). No young vegetative shoots were present for comparison in this species, but the mature vegetative stem, bearing strobili, shows the characteristic structure of the stem (fig. 19). The phloem is distinct and is recognizable earlier than in most of the species.

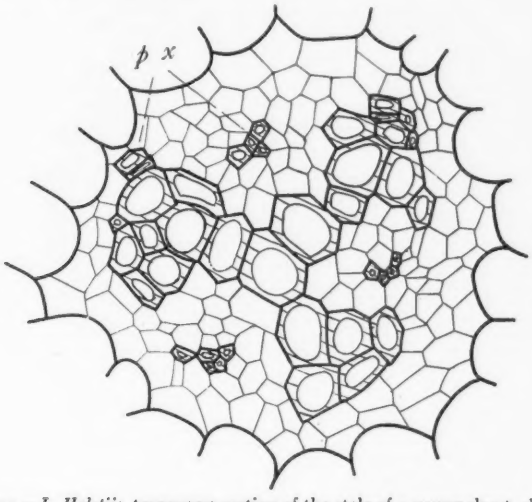


FIG. 22.—*L. Holstii:* transverse section of the stele of a young shoot, showing the radial arrangement; *px*, protoxylem; ×500.

Cortical roots occur toward the base of the stem as described in *L. carinatum*, but their structure is similar to those described for *L. pithyoides*.[1]

L. Holstii

The material of this species was entirely vegetative, and of the vegetative shoots there were very few young ones. From a study of a limited number of slides, it appears that the stele is organized with a rather large number of protoxylem points (about 8). The

[1] STOKEY, ALMA G., The roots of *Lycopodium pithyoides*. BOT. GAZ. **44**:57–63. *pls. 5, 6.* 1907.

central portion of the stele is occupied by large unlignified cells which are slowly thickened into metaxylem. The phloem seems to arise irregularly near the periphery and is not easily recognized when young. In the young shoot examined, the stele became radial toward the base (fig. 22). Here there were fewer protoxylem points also, 3 or 4 in number, and part way up the stem there was an isolated xylem strand as occurs in *L. Billardieri* (fig. 19). The

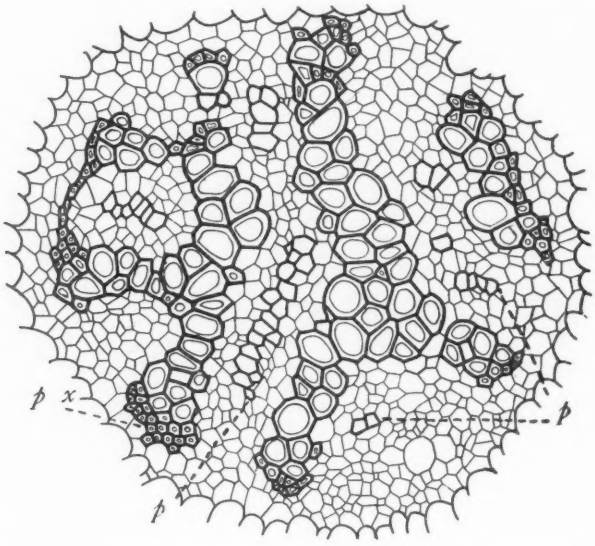


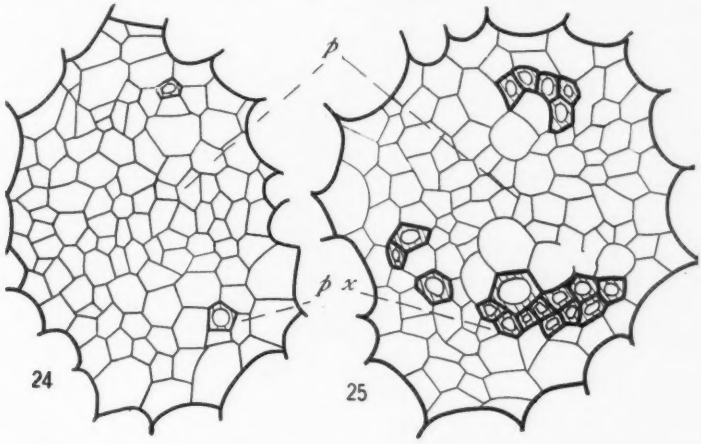
FIG. 23.—*L. Holstii:* transverse section of mature stem, showing parallel-banded type of stele; phloem scattered irregularly between the xylem bands; *px*, protoxylem; *p*, phloem; ×185.

distinctly radial arrangement extended to the base of the shoot where it joined the main plant.

In the fully mature vegetative stem there is an irregular parallel-banded type of stele (fig. 23) differing in appearance from that described for *L. verticillatum*, and more developed than those in the strobilus of *L. carinatum*. The phloem in the mature stele is scattered in patches throughout the parenchyma bands between the xylem groups.

L. verticillatum

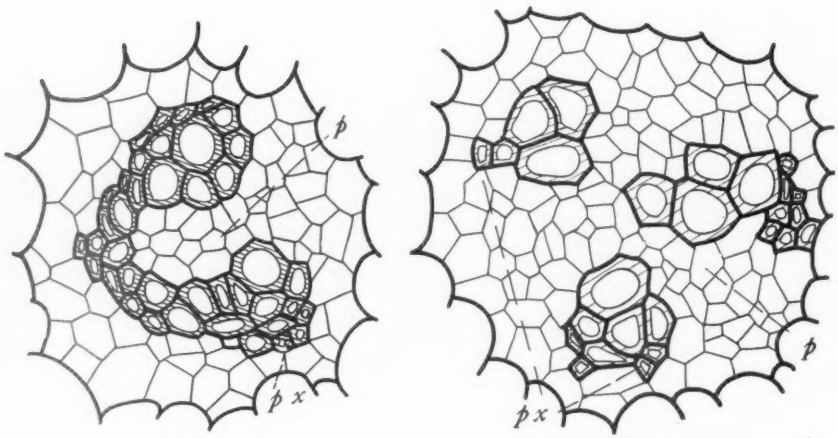
The stele of the strobilus in this species is characterized by the differentiation of very few protoxylem points, 2 or 3 groups being usual (figs. 24, 25). It differs from the other species in not being radial at the apex. The organization of the stele in the strobilus seems to be generally of the parallel-banded type from the first, with a phloem group between two xylem bands, as sometimes occurs in *L. varium*, and this develops into the crescent-shaped xylem mass with phloem in the middle, as has been described for



FIGS. 24, 25.—*L. verticillatum:* transverse sections in series, showing the protoxylem groups and the developing parallel bands; *px*, protoxylem; *p*, phloem; ×500.

the other species (figs. 9, 26). This crescent-shaped mass breaks up into the parallel-banded type, and then later at a lower level in the strobilus axis, the metaxylem begins to grow inward and breaks up the phloem band, forming a distinctly radial arrangement (fig. 27). The phloem in this species is very difficult to recognize, and often even in the mature stem the extent of the phloem is uncertain.

The mature vegetative stem is of an irregular parallel-banded type with rather numerous protoxylem points. The phloem is very limited in amount, and is scattered somewhat irregularly



FIGS. 26, 27.—Fig. 26, *L. verticillatum:* transverse section, showing the development of the crescent-shaped xylem mass from the parallel-banded arrangement; *px*, protoxylem; *p*, phloem; ×500; fig. 27, *L. verticillatum:* transverse section, showing the radial arrangement derived from the crescent-shaped xylem mass; *px*, protoxylem; *p*, phloem; ×500.

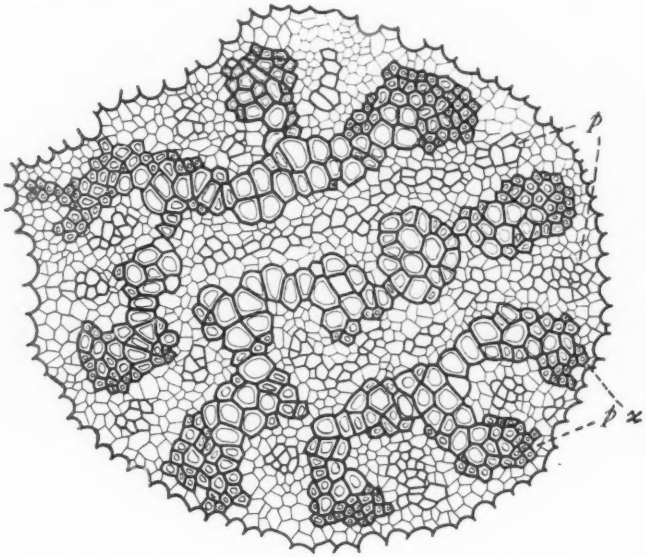


FIG. 28.—*L. verticillatum:* transverse section of the mature stem, showing the parallel-banded type of stele; *px*, protoxylem; *p*, phloem; ×185.

between the protoxylem points and between the xylem bands (fig. 28).

Discussion

JONES,[2] in an investigation of about a dozen temperate and tropical species of *Lycopodium*, found that the radial arrangement of the stele is very characteristic, especially in young plants. He says "the principal feature observed in sections of the young stem is that the vascular bundles present a triarch or tetrarch arrangement exactly similar to the structure which may be found in roots." He also states that it has always been suggested that this arrangement represents a very primitive type of stele. JONES also divides the mature stems into two categories: parallel-banded, connected with a high number of protoxylem groups; and a second type characterized by a promiscuous mixture of xylem and isolated phloem patches, which he regards as characteristic of tropical epiphytes.

HOLLOWAY,[3] in a study of the young sporophytes of six New Zealand species of *Lycopodium*, classifies them as follows in regard to the type of stele: (1) a "mixed" type, with indiscriminate mixture of xylem and phloem; (2) a radially banded type, with the radial arrangement of xylem and bands of phloem situated between the xylem radii; and (3) the parallel-banded type, with the xylem and phloem arranged in alternating bands across the cylinder. He notes that the radial and parallel-banded types are closely related and may pass into one another, and that the latter is associated with a relatively high number of protoxylem points, 5–9 he says being sufficient to give that arrangement.

WIGGLESWORTH,[4] from a study of young sporophytes of *L. complanatum* and *L. clavatum*, concludes that the radial arrangement of xylem and phloem occurring in upright forms of *Lycopodium* is the more primitive condition. In the upper part of the stem she

[2] JONES, C. E., The morphology and anatomy of the stem of the genus *Lycopodium*. Trans. Linn. Soc. II. **7**:15–35. *pls. 3–5*. 1905.

[3] HOLLOWAY, J. E., A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. N. Zeal. Inst. **42**:356–370. *pls. 32–34*. 1909.

[4] WIGGLESWORTH, GRACE A., The young sporophytes of *Lycopodium complanatum* and *Lycopodium clavatum*. Ann. Botany **21**:211–234. *pl. 22*. 1907.

found a triarch or tetrarch arrangement, with the three or four protoxylem groups connected with metaxylem, and in the base of the young plants there was a central core of xylem in the center of the stele.

BOODLE[5] investigated the stem structure of *L. volubile* and *L. salakense*. He regards the normal *Lycopodium* stele to be the parallel-banded type, as in *L. volubile*. *L. salakense* has the intermingling of xylem and phloem, resembling *Gleichenia*. He notes that in some cases the presence of the peripheral growth of the protoxylem forms a nearly continuous ring.

The present investigation extends the range of knowledge of the anatomical structure of *Lycopodium* by including some species not studied before, which show certain phases of stelar development to be especially emphasized. It emphasizes the fact that the radial arrangement of the stele is quite common, and that in many cases it is the original condition from which the parallel-banded type is derived. While this radial arrangement is probably the common one in *Lycopodium*, it is not the universal condition, and the great variability of the stelar structures in these epiphytic species deserves especial emphasis. It should also be kept in mind that the greater variability in structure occurs in the stele of the strobilus, while the vegetative steles remain relatively constant. The presence of a great variety of types of stele, radial, parallel-banded, crescentic, and that corresponding by definition to the amphivasal in the same plant, and even in the same stem, as occurs in *L. carinatum*, makes it clear that these types are more closely related than has been supposed.

JONES relates the parallel-banded type to the plagiotropic stems generally, but notes that there are some exceptions, as the orthotropic *L. obscurum*, which has the parallel-banded arrangement. HOLLOWAY points out that the parallel-banded arrangement is derived from the radial as a result of the branching stem. Both JONES and HOLLOWAY consider the radial arrangement characteristic of the stems of epiphytic species of *Lycopodium*.

[5] BOODLE, L. A., On the structure of the stem in two species of *Lycopodium*. Ann. Botany 14:315–317. 1900.

The present investigation shows that not all of the epiphytic species are characterized by the radial arrangement of the stele, since *L. verticillatum* has generally the parallel-banded type. Further, it shows that not only may both radial and parallel-banded types occur in the same stem, associated with crescentic and amphivasal, but that these changes from one arrangement to another are independent of the branching of the stem, as seen in *L. carinatum*, *L. Phlegmaria*, and *L. varium*. Branching does induce change from radial to parallel-banded arrangement, but this change may also occur without branching.

There seems to be a general opinion, as expressed by JONES and also by HOLLOWAY, that the parallel-banded type of stele is associated with a large number of protoxylem points, and this opinion may be completely justified by evidence drawn from the study of the young sporophytes. In the mature plants, in some of the species used in this investigation, the parallel-banded arrangement occurred where there were but 2, 3, and 4 protoxylem points; and in *L. verticillatum* the parallel arrangement started with but 2 protoxylem points. In these species the parallel-banded arrangement seems to be just as definitely associated with a small number of protoxylem points as in those studied by JONES and by HOLLOWAY, where it was associated with a large number.

BOODLE regards the parallel-banded arrangement as the normal *Lycopodium* stele, but from this study it seems unsafe to regard any particular type of bundle arrangement as normal, since it will depend upon the level at which the stem is cut, or how near the section is to the point of branching as to what type of stele is found, for all the known *Lycopodium* steles may be found in the same stem excepting the so-called "mixed" stele.

Attempts have been made to connect the factors determining the stelar development with the type of stele found in the various species of *Lycopodium*. Plagiotropism has been suggested as being the factor favoring the formation of the parallel-banded type of stele, and orthotropism that favoring the development of the radial stele, but so many exceptions are to be found to these statements that they seem to lose significance. The conditions

under which these epiphytic species grew are described as being about the optimum for vegetative growth. A definite structural evidence for rapid elongation in these plants is the close series in sporogenesis shown by serial transverse sections of the strobilus. It would seem then that these variations of stelar structure occur under conditions favoring rapid elongation. Whatever the conditions may be, the fact of the variations emphasizes the susceptibility of these species to conditions and the ability to modify the stelar development, which is generally regarded in most plants as rather a fixed structure.

Summary

1. From this investigation it may be concluded that the species of *Lycopodium* studied are characterized by great variability in the development and structure of the stele.

2. The radial stele may be considered as the prevailing type, and as the basis in most cases for modification to the other types found.

3. There are found radial, parallel-banded, crescentic, and amphivasal steles in the same strobilus axis in *L. carinatum*, and all types but the amphivasal in *L. Phlegmaria* and *L. varium*.

4. *L. Billardieri* is the most constant in its stelar structure, with a type of stele so characteristic as to make the species almost recognizable by the transverse section of the stem.

5. *L. verticillatum* has generally parallel-banded arrangement of stele, although the radial stele has been considered the prevailing type in epiphytic species.

6. All attempts to place the species of *Lycopodium* in definite categories based on the character of the stele are extremely uncertain, since there are exceptions in some species and even exceptions in different parts of the same stem in some species.

7. If the character of the stele is in any way dependent upon varying conditions, its use in phylogeny must recognize this fact.

8. The investigation confirms the idea that the radial arrangement of the stele, retained persistently by the root, is probably the most primitive stem arrangement, from which most known stems have departed.

This investigation was undertaken at the Hull Botanical Laboratory, University of Chicago, and was completed under the direction of the staff of that institution. The writer wishes to express his thanks to Dr. J. M. COULTER for his constant advice and criticism, and to Dr. CHARLES J. CHAMBERLAIN and Dr. W. J. G. LAND for the material furnished for the investigation and for their criticism of the preparations and aid in interpretation.

HULL BOTANICAL LABORATORY
UNIVERSITY OF CHICAGO

CURRENT LITERATURE

BOOK REVIEWS

Die Kultur der Gegenwart

During the past twenty years no botanist has appeared oftener in our "book reviews" and "notes for students" than EDUARD STRASBURGER. It is with a keen sense of loss that we write this final review.[1] In the spring of 1911 STRASBURGER wrote to the reviewer: "A year ago I felt compelled to participate in a work of great scope under the title of *Kultur der Gegenwart*, which is to present in accessible form the entire field of science. The object may be good in itself, but I have often regretted that I undertook the work and that I must devote to it, rather than to my research, the few years of scientific activity which still remain for me. I have not felt well the past winter, but nevertheless have had to work hard." About this time he wrote to TISCHLER that he was devoting eight hours a day to the work. The day before he died the manuscript was completed, and he also added the finishing touches to the manuscript for the third edition of his *Streifzüge an der Riviera*. With these two tasks out of the way, he was eagerly planning to take up his interrupted research, but his contribution to the *Kultur der Gegenwart* was destined to be his last.

The *Kultur der Gegenwart* is a work of even greater scope than STRASBURGER'S letter indicated, for it embraces not only the sciences, but also philosophy, law, history, and literature. Some of the titles, like "The religion of the orient," "The history of philosophy," "The Greek language and literature," "The history of law," "Mathematics in ancient and mediaeval times," "Chemistry," "Astronomy," "The transformation of energy," "Anthropology," "Mountain structure," "The technic of war," will give some idea of the range of knowledge one should possess if he is to be regarded as a man of culture at the present time. The entire work comprises 61 volumes. The present review deals only with Vol. 2 of the fourth section of the third subdivision, or III Teil, IV Abteil, Band 2. This method of designating volumes may be very clear to the German mind, but, like the endless "Teil" and "Abteil" of the *Pflanzenfamilien*, it is confusing to the American. We should have marked the present contribution Vol. 36, which seems to be its position in the series of 61 volumes. In this volume there are two sections: "The plant cell and tissues" by STRASBURGER, and "Morphology and development of plants" by BENECKE. The two contributions will be considered separately.

[1] Die Kultur der Gegenwart. Teil III. Abt. IV. STRASBURGER, EDUARD, Zellen und Gewebelehre; und BENECKE, W., Morphologie und Entwickelungsgeschichte. 8vo. pp. vi+338. Leipzig: Teubner. 1913. *M* 14.

THE PLANT CELL AND TISSUES.—The title is broad enough to cover most of the fields now designated as cytology and morphology. Some of the topics are: cell contents, cell membranes, nuclear and cell division, reduction of chromosomes, fertilization, alternation of generations, origin of tissues from apical cells and from meristem, differentiation of tissues, etc. Throughout the work the cell and tissues are treated not only from the standpoint of structure, development, and phylogeny, but also from the standpoint of chemical composition and function. While both vegetative and reduction mitoses are rather minutely described, little attention is given to conflicting theories. The main facts stand in bold relief, without those obscuring details which vary in different forms, or which may be present in some plants and lacking in others. In the treatment of mitosis, the chromosome is regarded as an individual organ. In the description of fertilization, the nucleus is regarded as the sole bearer of hereditary characters, so far as heredity is concerned, the cytoplasm being only the necessary medium in which the nucleus exercises its functions. Alternation of generations, of course, is regarded as antithetic; alternation is recognized in animals as well as in plants, in both cases the two generations being distinguished by the haploid and diploid number of chromosomes, a position with which the reviewer is in the heartiest accord. The origin of tissues from apical cells or meristem and the differentiation of cells into vessels, sieve tubes, sclerotic cells, glandular hairs, etc., is followed in many cases.

The work, as indicated by STRASBURGER's own words, was not intended as a piece of research. The object was to make such a presentation of the cell and tissues as a man of culture, although not a professional botanist, might read with profit. It can be said, without the slightest hesitation, that even the professional botanist can read it with profit, for it covers most of the field of cytology and morphology, and presents the views of one who speaks from an abundance of first-hand knowledge and who has contributed more to the subject than any other man of his generation. While the reading may be rather difficult for the average man who regards himself as cultured, it is hard to see where it could have been simplified. Such a presentation was no new experience for STRASBURGER, since he had for many years given his weekly Friday lecture to the people of Bonn. These lectures brought fundamental botanical problems within the reach of those who were interested enough to attend. The style is much simpler than STRASBURGER used in publishing his researches. This is seen particularly in the shorter sentences and in the comparative scarcity of technical terms. To the cytologist, the book is full of suggestions for research.

MORPHOLOGY AND DEVELOPMENT OF PLANTS.—The field left for BENECKE's contribution, after the broad presentation by STRASBURGER, would seem rather limited. The subject is treated under two subdivisions: (1) general, and (2) special. The first is devoted largely to a consideration of the form and function of the root, stem, and leaf, comparatively little attention being given to

reproductive structures, because vegetative structures can be presented without all sorts of details, and because reproductive structures lead so easily to general questions and plant systems. GOETH'S theory of metamorphosis is presented and a modified view of this theory seems to dominate the discussion. This general part occupies only 31 pages.

The second, or special part, presents the various groups from the algae up to the flowering plants, and occupies 120 pages. The reading should not be very difficult for an educated man, interested in botany, but not a professional botanist. The technical terms, especially those used in describing flowering plants, are rather numerous.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS

Recent work on tropisms.—For orthotropic organs FITTING and others have proved that geo-excitation increases with the sine of the angle of displacement from the normal or labile rest position. Therefore, the horizontal position gives maximum stimulation, and all equal displacements below and above it equal stimulation. NOACK asserts that this physiological response does not parallel any known change in the energy of gravity itself with variation of the angle, and is not capable of direct physical explanation.

NOACK[2] inquires whether photo-excitation of orthotropic organs obeys the sine of angle law. Assuming constant source of unilateral light, the intensity falling on a given surface of the plant organ varies as the cosine of the angle of deviation from the perpendicular, or as the sine of the angle of deviation from the rest positions. On the basis of light intensity, therefore, one might expect the sine law to hold. NOACK finds, however, that intensity of the illumination of the flank of the organ is not the sole factor, but the direction of the striking rays is important, hence the sine law does not apply. He studied chiefly the coleoptile of *Avena*. The following table shows the "Schwelle" (product of light intensity in candle-power actually falling on the illuminated surface of the organ by least time in seconds necessary to give a final response in 50 per cent of the organs) and presentation time under constant light source for the various angles of deviation from the normal rest position.

Angle	15°	30°	45°	65°	90°	105°	120°	135°	150°
Schwelle	7.3	9.5	11.9	11.18	12.2	15.8	20.3	23.7	32.4 (C.M.S.)
Presentation time	28.2	19.0	16.8	12.9	12.2	16.4	23.6	33.5	64.8

The "Schwelle" for the different angles shows the organ is more sensitive to impinging light from above than from below the horizontal, and that this sensitiveness increases continuously from the inverse to the normal rest position. This increase follows a regular law, as is shown by the fact that the product of

[2] NOACK, KONRAD, Die Bedeutung der schiefen Lichtrichtung für die Helioperzeption parallelotroper Organe. Zeitschr. Bot. 6:1–79. 1914.

the supplement of the angle of deviation from the normal rest position by the "Schwelle" is a constant. These facts indicate that the organ is most excited by light striking it from directly above, though of course this produces no response. The "Schwelle" for this position is calculated at 6.7 C.M.S. Some measurements were made also on the sporangiophore of *Phycomyces* and on the mustard seedling. In the latter, as in *Avena*, the "Schwelle" decreases as the angle of impinging rays passes from the inverse to the normal rest position, while in *Phycomyces* just the reverse behavior appears. With light striking the organs at right angles, mustard has a "Schwelle" of 240 and *Phycomyces* 60, against 12 C.M.S. for oats. NOACK believes he has settled a long-contested point by establishing that the direction of the impinging ray and not the difference in light intensity on two flanks is the determining factor in phototropism. He also takes his results as evidence for the polarization conception of FITTING in conduction of the phototropic stimulus. He believes photoperception and presention are too complex to be explained as simple photochemical reactions, as some have attempted to do.

BOYSEN-JENSEN[3] repeats and confirms his earlier experiments which showed that the conduction of the phototropic stimulus in the coleoptile of *Avena* is localized in the half of the seedling not illuminated. He reasserts that FITTING's conception of the polarization in all cells of the organ determined by the direction of the impinging rays is untenable, and finds no evidence for VAN DER WOLK's claim of wound effects compensating for phototropism.

RISS,[4] working in JOST's laboratory has devised a special sort of centrifuge for the purpose of studying the effect on orthotropic stems and roots of applying centrifugal force equilaterally at right angles to the longitudinal axis of these organs. Such application of centrifugal force, unlike unilaterally applied light, has no tonic effect on the plant organ. This finding is contrary to the assumption of BACH. Such equilaterally applied centrifugal force also causes no modification in the geotropic effect of unilaterally applied gravity, whether the former be applied before, during, or after the latter. In some cases the equilateral force was 20 times the unilateral. This leads to the important conclusion that WEBER's law does not apply to geotropic discriminative sensibility. Centrifugal force acting in the longitudinal direction inhibits the geotropic effect of a right angle stimulus. The action of gravity at an oblique angle on the orthotropic organ is not a result of the right angle components alone, but the effect of the latter is inhibited by the longitudinal components. For this reason, the author concludes that the sine of angle law of FITTING and BACH does not strictly apply even between 45° and 90°, although the deviation here is slight. The horizontal position of the organ is the position

[3] BOYSEN-JENSEN, P., Über die Leitung des phototropischen Reizes in der Avenakoleoptile. Ber. Deutsch. Bot. Gesells. **31**:559–566. 1914.

[4] RISS, MARIE-MARTHE, Über den Einfluss allseitig und in der Langsrichtung wirkender Schwerkraft auf Wurzeln. Jahrb. Wiss. Bot. **53**:157–209. 1913.

of maximum geo-stimulation both because gravity acts at right angles to the organ and because no longitudinal components are present.

DEWERS[5] has applied the PICCARD rotation method to determining the distribution of geo-sensitiveness in various plant organs.[6] In the root of *Lupinus albus* the greater sensitiveness lies in the terminal 2.5 mm. The hypocotyl of *Helianthus* always gives a permanent *S* response due to low irritability and slow conduction of the stimuli. The method does not determine the distribution of geo-sensitiveness in this organ. In *Hordeum vulgare*, *Panicum miliaceum*, and *Setaria italica*, the coleoptile is much more sensitive than the internode, although the internode is slightly sensitive in all these, most so in *Panicum*. The sensitiveness in the coleoptile of *Hordeum* is about equally distributed, so that when about half of the organ projects across the axis of the centrifuge an *S* response occurs which later entirely straightens out. Apparently there is about equal acropetal and basipetal conduction of the stimulus in the two directions. Whether this occurs by separate paths in the two directions is not known. The geo-irritability of the internode of *Panicum* is higher than that of *Sorghum*, while the reverse is true of photosensitiveness. In general, however, DEWERS finds that geo-conduction and photoconduction and reaction run parallel in these organs. In general, those organs that show quick perceiving power show rapid conduction, and those showing slow perceiving power show slow conduction. The coleoptile of *Hordeum* belongs to the first class, and the hypocotyl of *Helianthus* to the second. In an "Anhang" the author reports that he was unable to find a destarching agent, for the purpose of throwing some light on the statolith theory, the application of which did not greatly injure the root. He tried Al_2Cl_6 and $Al_2(SO_4)_3$ alone and in combination with Knop's solution and KH_2PO_4.

PORODKO[7] has studied chemotropic response of roots to various alkalies and alkali earth salts. The experiments consisted of a square millimeter of filter paper saturated in the salt solution applied to the side of the roots in darkened moist chambers. In lower concentrations positive chemotropic responses occurred; in higher, negative chemotropic responses; and in still higher positive, chemo-traumatic responses. PORODKO asserts that the first response is a true tropic response, for perception is localized in the tip, bending is due to growth, and the concentration producing the response is comparatively low. It is also not osmotropic, for the concentrations producing it in the various salts show great variation. The positive and probably the negative response is due to the action of ions. The effect of the ions beginning with those most effect-

[5] DEWERS, F., Untersuchungen über die Verteilung der geotropischen Sensibilität an Wurzeln und Keimsprossen. Beih. Bot. Centralbl. **31**[1]:309–357. 1914.

[6] For methods see BOT. GAZ. **47**:482, 483. 1909; and PFEFFER'S Plant physiol. Eng. ed. **3**:419.

[7] PORODKO, TH. M., Vergleichende Untersuchungen über die Tropismen. Ber. Deutsch. Bot. Gesells. **32**:25–35. 1914.

ive is (1) for positive response, tartrate>citr.>SO_4>acet.>ClO_3>Cl>NO_3>J >CNS; Rb>Cs>K>Li>Na; (2) for negative response, (*a*) for alkali salts, acet.>tartr.>J>Cl>Citr.>ClO_3>CNS>SO_4>NO_3; Na>Li>K>Cs>Rb; (*b*) for salts of alkali earths, J>Br>acet.>Cl.; Mg>Ca, Ba, Sr.

The bromide and perhaps the iodide of alkali earths do not produce the positive response. For negative chemotropism, salts of alkali earths are about 10 times as effective as those of the alkalies. PORODKO believes from the relative effectiveness of ions that the negative excitation involves coagulation of cell lipoids as well as proteins, and that both the positive and negative irritability are lined up with change of condition of cell colloids. Our knowledge in this field is too limited, however, to follow the parallel in any detail.—WILLIAM CROCKER.

A theory of evolution.—Lest we forget that the method of evolution remains undemonstrated, that evolution itself is somewhat of a scientific dogma, it is desirable occasionally to have our attention called to the fact that scarcely two even of the clearest-headed of our contemporary thinkers hold the same views regarding it. Read BERGSON, BUTLER, DEVRIES, SEMON, WEISMANN. Their works are lawyers' briefs, written to uphold the importance of a single possible evolutionary cause to the greater or less neglect of all others; but they are remarkable briefs for all that. Evolution is due entirely to a directive force within the organism; evolution is due wholly to imperfections in the machinery of heredity and has no directive aim whatever; evolution is due solely to external causes; it is gradual, it is discontinuous; it is continual, it is periodic. One is often led to believe that no middle ground, no combination of methods is possible; moreover, it is often the individuals that strum continually on a few notes, who force recognition of tunes labeled conspicuously with their own personalities, by loud and persistent reiteration.

The latest writer to be enrolled as an exponent of a unique cause of evolution is LOTSY.[8] The unique cause is hybridization and the author's brief has been extraordinarily well done. As the paper is introduced by the following statement, the words "unique cause" do not exaggerate the position taken:

> Toutes les théories de l'évolution, y compris celle de Lamarck, Darwin et DeVries, s'appuient sur l'hypothèse, ou sur la prétendue preuve, qu'il existe d'une façon ou d'une autre une variabilité héréditaire. Le présent travail a pour but de prouver que cette hypothèse se base sur une erreur; qu'il n'y a pas de variabilité héréditaire, sous aucune forme, mais que les expèces sont constantes.

LOTSY does not believe that Linnean species are constant, but that forms truly homozygous are constant. His outline of the growth of evolutionary belief shows this.

A. The period when it was believed that the characters of an individual were transmitted as a whole.

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[8] LOTSY, J. P., La théorie du croisement. Arch. Néerland. Sci. Exact. et Nat. III B 2:1–61. 1914.

a) The idea that Linnean species form a natural system.
1. Belief in the constancy of Linnean species.
2. Belief in the variability of Linnean species.
b) The idea that the elementary species of JORDAN form a natural system.

B. The period in which proof was given of the independent transmission and chance recombination of characters.
a) Belief in the variability of JORDAN'S species: the theory of mutation.
b) Belief in the constancy of JORDAN'S species: the theory of crossing.

LOTSY'S arguments are based upon the following assumptions, on each of which there is room for a difference of opinion: (1) that all characters obey the Mendelian law of heredity, (2) that acquired characters are never transmitted, (3) that homozygotes are absolutely constant in successive generations, (4) that there has been no proof of variation independent of crossing, and (5) that the variations observed after crossing are sufficient to account for evolution.

The first point is taken for granted, although there are certain to be many objections to it raised. Even the most ardent Mendelians have only gone so far as to assert the generality of Mendel's law in the sense that the transmission of many characters is controlled by some mechanism that is widespread in the animal and plant kingdoms, probably the chance apportionment of the chromosomes to either of the two daughter cells at the reduction division. The probability that there are many cases where such a mechanism is replaced by others can hardly be denied, though JENNINGS' recent investigations on paramecium indicate a generality of segregation hitherto unsuspected. Furthermore, even in cases where Mendel's law might be expected to be valid from other considerations, as in the Oenotheras, there appear to be independent or subsidiary laws at work which modify the results.

Perhaps most biologists admit that the inheritance of acquired characters has never been proved experimentally; on the other hand, it may be that it is impossible to prove that the hour hand moves in an experiment covering a second of time, as BUTLER very aptly puts it. Is it not justifiable, therefore, for experimentalists to assume non-inheritance of acquired characters as a practical working hypothesis for experimental biology, and just as permissible for evolutionists to assume their transmission over long periods of time, provided it is granted that this is a mere assumption? LOTSY applies the *negative* conclusions of experimental biology to evolution, a method that is always open to criticism.

The contention that homozygotes are absolutely constant in all succeeding generations is also disconcerting. The conclusion is drawn largely from JOHANNSEN'S work, yet JOHANNSEN believes in mutations. But even leaving out of account the sudden changes that have appeared in material apparently homozygous, there are those who believe that the pure line work does not show constancy in succeeding generations. CASTLE, for example, who does not come to a conclusion without due consideration, believes that selection

may always modify a homozygous character. The reviewer, taking a middle ground, believes that the pure line work least subject to criticism, that on self-fertilized material, does prove homozygotes to be sufficiently constant in succeeding generations to make this constancy a basis for mathematical description, but he believes it to be unbiological to assert this constancy as absolute.

As the basis of his assertion that there has been no proof of variation independent of crossing, the author notices only the work of DEVRIES. Undoubtedly there is a great deal in favor of the idea that the *Oenothera* mutants are the results of segregation from crosses, though the phenomena have not been fitted into present Mendelian concepts. But that the very fine contributions of DAVIS and HERIBERT-NILSSON on this subject have clinched the matter, as LOTSY believes, would not be asserted, I venture to say, by the authors themselves. It is pointed out very clearly that both the constructive work of GATES in defense of the *Oenothera* mutations and his criticism of HERIBERT-NILSSON are not so conclusive as that author so confidently asserts, but this is only negative evidence. Moreover, the work of MORGAN, JENNINGS, BATESON, and others on the occurrence of mutations in controlled cultures is complacently neglected.

LOTSY'S own extensive work on specific crosses in the genera *Nicotiana*, *Petunia*, *Pisum*, and *Antirrhinum*, the constructive work of the paper, is exceedingly interesting, and his detailed accounts, which are in press, will be eagerly awaited. In brief, all the inter-specific crosses that he has undertaken have shown true Mendelian segregation. The conclusion of DEVRIES, drawn from the peculiar behavior of the *Oenothera* species, that inter-specific and intra-specific crosses obey different laws of heredity, is shown, therefore, not to be of general validity.—E. M. EAST.

Cecidology.—Among the very important contributions to European cecidology are HOWARD'S papers on the collection in the Museum of Natural History in Paris[9] and from Western Africa,[10] all of which are taxonomic in character and well illustrated. The author uses the modern method of grouping the galls with reference to the host plants, which makes the data available to those botanists who are interested in the study of malformations of plants and in the relation of plants to other forms of life.

ROLL HOWARD[11] presents an exceptionally good paper on the anatomy of the galls on the margins of leaves. He divides these malformations into four groups; those caused (1) by hypertrophy and hyperplasia, (2) by hyperplasia,

[9] HOWARD, C., Les collections cécidologiques du laboratoire d'entomologie du muséum d'histoire naturalle de Paris: Galles de Burséracées. Marcellia **12**:57–75. 1913; also Galles d'Afrique et Asie **12**:102–117.

[10] ———, Les Galles de l'Afrique occidentale française. VI. Cécides du haut Sénégal-Niger. Marcellia **12**:76–101. 1913.

[11] HOWARD, ROLL, Recherches anatomiques sur les Cécidies foliaires marginales. Marcellia **12**:124–144. 1913.

(3) by hypertrophy, (4) by atrophy. This paper is well illustrated and leads the thoughtful American botanist to realize the enormous amount of research work that could be carried on in this country on this one branch of cecidology or plant pathology.

The recent American literature presents a paper by PARROTT and HODGKINS[12] in which the authors describe the pathological condition caused by the false tarnished plant-bug (*Lygus invitus*). This pest attacks the fruits before they are one-half inch in diameter, causing many of them to fall. The injury is said to be quite characteristic. "As the pears grow, the outer layer of the skin about these spots becomes ruptured, and a light-yellow, mealy-appearing growth of the inner layers of skin protrudes, making more or less triangular, granular spots; or when two or more spots run together a patch or crack lined and bordered with corky tissue. The yellowish, protruding growth at first makes a marked contrast with the smooth green skin of the little pear; and later the cessation of growth at these points causes depressions and marked general deformity of the fruit. In the flesh beneath, also, hard, gritty granulations are produced, through which it is difficult to cut with a knife." This paper illustrates another broad field of plant pathology and physiology which is practically untouched by American botanists.

One of the most satisfactory pieces of scientific cecidology of recent years is TRIGGERSON'S[13] work on *Dryophanta erinacei*. The author begins his study with the well known *Acraspis erinacei* or hedgehog-gall which occurs on the white oak, and proves it to be caused by a dimorphic species of insect. The insects from this gall are agamic and oviposit on the leaf and flower buds of the same host, causing an entirely different gall giving rise to the sexual form which belongs to the genus *Dryophanta*. The author also gives the results of some very interesting studies of the parasites and inquilines, and finally some studies leading to the conclusion that the stimulus is due to a fluid secreted by the malpighian vessels of the larva. However, comparative studies indicate that this is not necessarily true in the case of other galls. The physiological side of this paper will be of great interest to those plant physiologists and pathologists who can overcome their prejudice long enough to give it careful consideration.

Another exceptionally good piece of work which is strictly botanical is by STEWART[14] and treats of the anatomy of the black knot (*Plowrightia morbosa*). The author finds that these knots may originate from spore infection from

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[12] PARROTT, P. J., and HODGKINS, H. E., A pear-deforming plant bug. New York Agricultural Experiment Station (Geneva) Bull. 368. 1913.

[13] TRIGGERSON, C. J., A study of *Dryophanta erinacei* (Mayr) and its galls. Annals Ent. Soc. America **7**:1–34. *pls. 11.* 1914.

[14] STEWART, ALBAN, The anatomy of other features of the black knot. Amer Jour. Bot. **1**:112–125. 1914.

mycelium spreading from old knots; the fungus during the first year penetrates nearer to the pith in the distal than the proximal end, and the greatest disturbance is in the vicinity of the leaf gaps; in the case of the choke cherry, which was the host used in these studies, the multiseriate rays become broadened, the production of xylem elements is greatly inhibited, and the production of parenchyma stimulated. There is also a stimulation of the cambium accompanied by the misplacing of certain elements. The reviewer will add that many of the data given in this paper are homologous with those derived from the study of insect cecidia. The American botanical literature is very deficient in studies of pathological tissues, and it is to be hoped that this paper will stimulate research in this long-neglected field.

COSENS[15] gives a paper which is very suggestive to botanists, in which he says: "One fundamental and far-reaching principle of gall-production by insects is that the stimulus does not endow the protoplasm of the host with power to produce new types of organs, tissues, etc. Structures are in many cases originated that are not found on the same part of the normal host, but invariably their prototypes are present on another part of the plant or nearly related species. The protoplasm is so stimulated that not only are dormant characteristics strengthened, but also in certain cases latent properties are called into activity, and thus the apparently new type of production appears in the host." The author gives evidence from the study of several galls supporting this principle.

Among other American papers which should be mentioned is a valuable key for determination of the midge galls on the hickory by FELT;[16] and a very interesting biological paper by the same author[17] on adaptations; and also several systematic papers by the same author.[18] There should also be noted three valuable taxonomic papers by BEUTENMÜLLER on the acorn galls[19] and on new species of the Cynipideae.[20]—MEL T. COOK.

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[15] COSENS, A., Insect galls. Canad. Ent. **45**:380–384. 1913.

[16] FELT, E. P., Table of hickory leaf midge galls. Bull. Brooklyn Ent. Soc. **8**:98–99. 1913.

[17] ———, Adaptation in gall midges. Canad. Ent. **45**:371–379. 1913.

[18] ———, Three new gall midges. Canad. Ent. **45**:305–308. 1913.

———, Description of gall midges. Jour. N.Y. Ent. Soc. **21**:213–219. 1913.

———, Gall midges in an aquatic or semi-aquatic environment. Jour. N.Y. Ent. Soc. **21**:62, 63. 1913.

———, The gall midge fauna of New England. Psyche **20**:133–146. 1913.

[19] BEUTENMÜLLER, WILLIAM, The North American acorn galls with descriptions of new species. Bull. Brooklyn Ent. Soc. **8**:101–105. 1913.

[20] ———, A new species of *Neuroteras* from Washington. Canad. Ent. **45**:280–282. 1913.

———, Descriptions of new Cynipidae. Trans. Amer. Ent. Soc. **39**:243–248. 1913.

Subantarctic vegetation.—Of the several antarctic regions whose vegetation has been recently studied, South Georgia seems of particular interest, both because of its isolation and on account of the character of its vegetation, being transitional between the truly antarctic type and the well developed subantarctic associations found in such regions as the Falkland Islands. As a result of visits to the island in 1902 and in 1909, SKOTTSBERG[21] gives an interesting account of the plant associations. The island is mountainous, some peaks reaching 2000 m., and is largely covered with ice in the form of glaciers moving down the valleys and reaching the sea in fiords. There is little seasonal difference in climate, the summer mean temperature being about 4° C., and the winter about −1° C. Exposure is a factor of prime importance in determining the distribution of the vegetation. Only 15 species of seed plants and three ferns are found upon the island, but the moss and lichen floras are comparatively rich, with 99 and 58 species respectively, of which 46 and 24 respectively are endemic.

The principal plant associations are the tundra, the swamp and the tussock grass. The tundra has by far the most extensive development, showing all transitional forms from one rich in grasses to the moss-lichen carpet. The swampy places are dominated by Juncaceae, while the halophilous *Poa flabellata* tussock-grass association fringes the beach. It is often almost pure, the tussocks attaining a height of 1.5 m., with an equally great diameter. This association was formerly more widespread and equally important in the Falkland Islands,[22] but has been disturbed and largely destroyed by the introduction of sheep.

These islands have a comparatively mild climate of insular type. The summer mean temperature is 10° C., the winter mean 2°.5 C., affording a fairly well marked periodicity, especially in the flowering of the seed plants, although the 73 cm. of precipitation are very evenly distributed. In portions of the islands there is little snow, and the soil is never frozen hard, but, apparently because of very high winds, there are no trees. Nevertheless, 47 of the 162 species of vascular plants are evergreen. The possible land connection with the mainland during the Tertiary may account for 82 per cent of the species being Magellan plants; 15 species are endemic. SKOTTSBERG decides that the vegetation, because of its close peat-forming character, is really a heath, exhibiting many characters in common with the heaths of northern Europe, and particularly with that of Faeröes, although with grasses forming a more conspicuous element. The most widespread association is that dominated by *Cortaderia* and other grasses, largely of tussock habit. It seems to occupy

[21] SKOTTSBERG, C., The vegetation in South Georgia. Wiss. Ergeb. Schwed. Südpolar. Exped. 1901–1903. **4**: Lief. 12. pp. 36. *pl. 6* and *map*. 1912.

[22] ———, Botanische Ergebnisse der schwedischen Expedition nach Patagonium und dem Feuerlande 1907–1909. III. A botanical survey of the Falkland Islands. K. Svensk. Vetensk. Handl. **50**: 129. *pl. 13* and *map*. 1913.

much of the non-swampy ground where the subsoil is composed of finer material. Above the coarser dry soils the *Empetrum* heath association dominates with an abundance of low evergreen shrubs. In wet depressions the Falkland representative of the peat bog occurs in the *Astelia* association, where several seed plants replace *Sphagnum* and forming low absorptive cushions are largely responsible for the immense layers of peat, several meters thick, that furnish the only fuel on the islands.

The tops of the highest mountains (only 700 m.) are covered with *Empetrum* heath, but a semialpine character is given to the vegetation by the presence of many cushion plants, among which the two remarkable umbelliferous genera *Bolax* and *Azorella* are conspicuous.

The author gives interesting notes on the flowering of many species, and also classifies the plants according to the "biological types" of RAUNKIAER. He points out that the results hardly support RAUNKIAER'S characterization of the islands as possessing a "chamaephyte climate," in spite of the large percentage of chamaephytes and hemicryptophytes, since both classes are evergreen in the Falklands, showing slight vegetative periodicity, simply some arrest of growth during the winter. Among the numerous other interesting facts regarding various phases of the vegetation, the presence of a very considerable number of ferns belonging to the rainy west coast of Chile and Fuegia is worthy of notice, and is made conspicuous upon the map of the author's travels.

Tierra del Fuego[23] shows the passage of the grassy heath to the steppe, a transition to deciduous forest dominated by *Nothofagus pumilio* and in higher altitudes by *N. antarctica*, while the western half is covered with an evergreen rain forest in which *N. betuloides* and *Drimys Winteri* are the chief members. The distribution of these formations is shown upon an excellent map which has been extended in a more recent publication[24] to include South America to latitude 41° S. The evergreen rain forest is shown to extend to 48° S. without striking change. Within this southern extension of rain forest, the number of species is small and the precipitation so evenly distributed that little periodicity seems to be shown. On account of the rather sudden change due to a great increase in the number of species, SKOTTSBERG has selected the parallel of 48° S. as the northern boundary of the Magellan province of the subantarctic region. North of this line, not only is the forest richer in species, but there is more periodicity on account of the more unequal distribution of the precipitation. The rain forest extends to the eastern slopes of the Andes through several

[23] SKOTTSBERG, C., Pflanzenphysiognomische Beobachtungen aus dem Feuerlande. Wiss. Ergeb. Schwed. Südpolar Exped. 1901–1903. **4**: Lief. 9. pp. 63. *pl. 3* and *map*. 1909.

[24] SKOTTSBERG, C., Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. I. Übersicht über die wichtigsten Pflanzenformationen Südamerikas S. von 41°, ihre geographische Verbreitung und Beziehungen zum Klima. K. Svensk. Vetensk. Handl. **46**: no. 3. pp. 28. *map*. 1910.

valleys and usually passes by a transitional deciduous forest to the steppes of Patagonia.

HAUMAN-MERCK[25] has studied the northern part of this forest, and finding it quite different from the southern portion would separate the two along the parallel 46°S. into the Magellan and Valdivian forests, the latter extending to 36°S. and being distinguished by the richness of its flora as well as by the diversity of its species. At Valdivia, near the center of the area, the annual precipitation is 266 cm., well distributed. Some idea of the climate may be obtained from the fact that while peaches and grapes will not ripen, apples, plums, and potatoes grow readily, while there are also plenty of bamboos and bromeliads. While the mountainous character gives considerable diversity, the greater portion of the valleys and slopes is covered with a luxuriant evergreen forest of subtropical aspect, extremely rich in species. The different strata of the forest are well marked. Trees of the first size, 20–30 m. in height, overtopping dense stands of smaller size, represent comparatively few species, *Eucryphia cordifolia* and the largest of the evergreen beeches, *Nothofagus Dombeyi*, being most widely distributed. Quite as remarkable for their endemic character and for their local abundance are *Aextoxicum punctatum*, *Saxegothaea conspicua*, *Podocarpus nubigena*, and *Fitzroya patagonica*, the last being most important as a lumber tree. Many families are represented in the trees of second size, but none more conspicuously than the Myrtaceae, which contributes 30 species, including shrubby forms of *Eugenia*, *Myrtus*, and *Myrceugenia*. The legumes are conspicuously absent and *Drymis Winteri* is probably most abundant. The shrubs comprise many species, and like many of the trees often possess attractive flowers. Special mention should be made of the abundant bamboos, some developing the climbing habit and all belonging to the genus *Chusques*. Other climbers are fairly abundant and many, like *Hydrangea scandens*, are very beautiful when in flower. Epiphytes are abundant, but mostly limited to ferns, mosses, and lichens. At least 10 species of *Hymenophyllum* were noted. Other ferns are common among the epiphytes and dominate the herbaceous vegetation of the soil, *Blechnum*, *Dryopteris*, and *Asplenium* being prominent genera. Mosses penetrate the deepest forests, two particularly large and beautiful ones being *Polytrichum dendroide*, 30 cm. high, and *Hypopterygium Thouini*, 10 cm. high.

Of the many problems of this interesting area, the occurrence of a large deciduous beech, *Nothofagus obliqua*, in the midst of an otherwise evergreen forest, and the extension of the forest upon the eastern slopes of the Andes appear particularly fascinating. The transition of this eastern extension to the semidesert of Patagonia receives a portion of the author's attention, as does the distribution of *Librocedrus chilensis*, and the character of the alpine flora.—GEO. D. FULLER.

[25] HAUMAN-MERCK, L., La forêt-valdivienne et ses limites. Rec. Instit. Bot. Léo Errera 9:347–408. 1913.

Development of fern prothallia.—Working under KLEBS, ISABURO-NAGAI[26] gives further evidence, through an investigation of the physiology of fern prothallia, in support of the idea that the course of development in plants is largely dependent upon and influenced by external factors. The author divides his work into four parts, dealing respectively with the germination of the spore, the development of the prothallium, the production of rhizoids and sex organs, and the formation of adventitious branches.

The paper gives an exhaustive summary of previous investigations dealing with the prothallium in ferns, and describes also a considerable amount of original investigation carried out with a view to ascertaining the effect of external conditions upon the qualitative and quantitative courses of development of the gametophyte. By far the most interesting and significant feature of the work is the extent to which the investigator is able to induce or inhibit the formation of sex organs, the appearance of apogamy, and finally of adventive shoots. Interesting, too, but possibly of less significance, are the changes of form which he seems able to produce in the thallus.

He finds, for instance, that where the nutrient solutions on which the spores are germinated are poor in potassium, magnesium, and calcium, both antheridia and archegonia may be formed; on the other hand, while antheridia may be formed quite readily in a solution containing little or no nitrogen, the production of archegonia cannot take place. In other forms, where germination and vegetative growth go on in darkness as in light with equal facility, no antheridia are set in the former instance. The experiments further point to a direct connection between the concentration of the nutrient solution and the production of sex organs, since under scant illumination archegonia are not developed in the weaker concentrations. Still other results indicate that if the prothallium be kept under conditions favoring vegetative growth, sex organs will not appear; and the author concludes from this that sex organs are produced only on prothallia whose vegetative growth has been hampered (ameristic prothallia).

In this connection, ISABURO-NAGAI brings up the question of the distribution of sex organs, pointing out the fact that whereas the antheridia are generally scattered over the entire prothallial surface, the archegonia are restricted to the meristematic region around the notch. His explanation of this situation, however, is far from satisfactory, and will need considerable experimental backing before it is given general acceptance. Briefly, the author first remarks the difference between the egg and the sperm, in that the latter is poor in albumen, with which the former is abundantly supplied; secondly, that the cells of the apical region of the prothallium are also rich in albumen; and thirdly, that the archegonia are probably restricted to this apical region because they derive their excessive protein supply from the meristematic cells.

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[26] ISABURO-NAGAI, Physiologische Untersuchungen über Farnprothallien. Flora **106**: 281–330. *figs. 18.* 1914.

If this be true, it is probably the only case on record where the actively dividing members of a meristem act as nurse cells.

One of the most striking experimental results ISABURO-NAGAI publishes concerns his control of the formation of adventive branches. While he is unable to duplicate the results of HEILBRONN[27] in inducing adventive branching by exposing the prothallia to such narcotics as ether and chloroform, he finds that plasmolysis of the cells of the gametophyte will induce luxuriant formation of the vegetative shoots. In his explanation of this fact he makes the statement that the stimulus of plasmolysis is a purely physical one, consisting probably of the withdrawal of water from the cell. The possibility of this stimulus being chemical in its nature is precluded, because plasmolytic agents of widely different chemical nature all produce the same effect. He believes, also, that this is not a traumatic response, since wounding the thallus with a fine needle will not produce or stimulate the production of adventive branches. He accepts as a solution of the question the explanation of KLEBS who claims that the normal cell growth, at first rapid, is checked by the formation in the cell sap of deleterious substances. These are either withdrawn in the plasmolysis, allowing the initiation of renewed and vigorous growth when once the cell has returned to the normal condition, or else they are rendered inactive by the concentration of the cell sap during plasmolysis. A further hypothesis is that the growth of the older cells is checked by the younger cells through the direct protoplasmic connections between the two; that plasmolysis ruptures these connections; and that, therefore, upon the return to the normal condition vigorous growth may be resumed.

The investigation is concluded with a few additional facts on the influence of light upon germination, which are of no particular significance, inasmuch as they merely add a few names each to the lists of those spores which can germinate in darkness, and those which cannot.—HERMANN B. DEUTSCH.

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[27] HEILBRONN, A., Apogamie, Bastardierung, und Erblichkeitsverhältnisse bei einigen Farnen. Flora **101**:1–42. 1910.